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COMPARATIVE AUTECOLOGY OF CASSIOPE SPP. AT TREELINE IN JASPER NATIONAL PARK, ALBERTA

by

© JOHN EDWARD HARTER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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DEPARTMENT OF BOTANY

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External Examiner

Date. March 26, 1981.....

DEDICATION

To my parents, Vern and Joyce Harter,
who gave so much.

To my friend, Jim Mayo, who helped me
see the Shining Mountains through
the tall grass.

ABSTRACT

In the Canadian Rocky Mountains, Cassiope mertensiana (subalpine/maritime) and C. tetragona (artic-alpine/ continental) are major components of the healthland vegetation that is characteristic of high latitude treeline areas. The two species show niche separation along the complex gradient of elevation-exposure, in part related to physiological differences in plant water relations and cold hardiness.

Cassiope mertensiana occupies protected subalpine sites where early (October) and deep (>1.5-2.0 m) snow accumulations provide mild winter conditions. Transplants in more exposed tundra sites experience lethal desiccation and low temperature injury. Plants are cold hardy to only ca. -26°C and require the protection of snow cover in severe northern winters. Late snow release (early July) reduces the potential of summer drought, but atmospheric moisture stress can cause midday reductions in turgor and stomatal closure even at high soil water potentials. Shoot growth is reduced in sites of earlier or later snow release and at higher elevations. Greater leaf longevity (5-7 yr) than C. tetragona (2-3 yr) may give it a competitive advantage in protected sites.

Cassiope tetragona occupies moderately exposed sites in the low alpine zone. Variable early winter snowfalls frequently subject plants to desiccating conditions and low temperatures (<-25 to -30°C). Plants can tolerate short

periods of xylem sap cavitation and subsequent tissue dehydration (ψ_L to -6.0 MPa). Apical leaves are effectively sealed by glandular secretions and frequently survive severe desiccation. Plants are cold hardy to below minimum winter air temperatures. Moderate snow accumulations (0.5-1.0 m) result in June snow release and a potential of late summer soil drought. Compared to C. mertensiana, plants are more tolerant of atmospheric and soil moisture stress due to the relatively elastic cell walls of current leaves which maintain positive turgor at low water potentials. Shoot growth is favored by early snow release although winter survival is reduced in such sites.

The evergreen habit and conservative growth strategy conveys certain advantages in treeline environments, but requires winter snow cover for the protection of erect tissues. The greater physiological tolerances of C. tetragona may explain why it is more widespread in northern alpine regions and the Arctic.

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I. INTRODUCTION

At high altitudes and latitudes environmental severity increases; low air and soil temperatures, short growing seasons, and high wind speeds place restrictions upon plant growth and overall species diversity. Beyond the closed forest, tree growth and survival are reduced until at treeline (krummholz with supranival leaders) this life form becomes climatically limited. Treeline is a significant boundary in nature separating two fundamentally different ecosystems; one dominated by tree species and the other dominated by shrubs and herbs (Wardle 1974).

Tundra environments, while selecting against trees and annuals, favor long lived perennials that either possess evergreen leaves or rapidly produce new leaves by re-allocation from extensive food reserves (Bliss 1971, Callaghan and Collins 1976). Evergreen shrubs of several heath families are a major component of the treeline vegetation throughout the world and often characterize this zone (Bliss 1979, Specht 1979). At higher latitudes in the Northern Hemisphere, *Cassiope* dominated heathlands are a major component of this forest-tundra zone vegetation. This study examines the factors that influence the distribution of two species of *Cassiope* at treeline in the Canadian Rocky Mountains.

A. Limitations to Tree Growth at Treeline

To aid in understanding the dominance of shrubs at treeline it is necessary to consider the limitations to tree growth in this zone. Alpine and arctic treeline areas in the Northern Hemisphere have been linked by continuous routes for plant migration during the Quarternary era and are floristically related. Evergreen conifers of several genera including Abies, Picea, and Pinus are widespread (Baig 1972, Wardle 1974), but deciduous genera (primarily Larix and Betula) are important in many areas (Richards 1981).

Numerous hypothesis have been proposed to explain the alpine treelines (see reviews by Griggs 1946; Daubenmire 1954; Tranquillini 1976, 1979; Wardle 1971, 1974). Most of these hypotheses involve a factor complex that includes plant carbon and water balance, snow, wind, air-soil temperature, and mycorrhizal fungi. Early studies showed the correspondence of arctic and alpine treelines with the 10°C isotherm for the mean temperature of the warmest month (Brockmann-Jerosch 1919). This suggests a "heat deficiency" affecting the CO_2 balance of trees so that only respiration requirements are met and photosynthates are inadequate to maintain a large mass of non-productive woody tissue. The "heat deficiency" idea was also involved in an early hypothesis that the maturation of shoots of woody plants at high altitudes was impaired, giving inadequate resistance to winter desiccation (Michaelis 1934a,b). The involvement of winter desiccation has been indicated by many studies

(Schmidt 1936, Larcher 1957, Lindsay 1971, Hansen and Klikoff 1972) but it is not universal (Slatyer 1976, Marchand and Chabot 1978, Kincaid and Lyons 1981).

Several of the hypothesis proposed to explain alpine treelines are related and are integrated into models by Wardle (1974) and Tranquillini (1979) centered on evergreen conifers and involving summer and winter conditions. Various internal and external factors reduce summer CO_2 uptake by trees at high elevations which place restrictions on leaf, shoot, and root growth, and seed production, with resultant negative feed-back effects. In seasons of poor growth or at higher elevations, tissue maturation is impeded. Incomplete lignification or late terminal bud formation increases the chance of damage by low temperatures in early winter. The incomplete development of shoot primordia in terminal buds reduces growth increments in the subsequent growing season. The incomplete cuticular development on leaves increases transpiration and results in winter desiccation. The krummholz growth form is a result of winter and spring desiccation of leaves and buds. Above a certain altitudinal zone, evergreen tree species can only exist in the warm microenvironments near the ground surface and in microsites of winter snow cover where desiccation is avoided.

Deciduous trees at treeline maintain upright growth and often form an open woodland above the limits of sympatric evergreen species. The deciduous habit conveys certain advantages over evergreenness during the winter which are offset by summer disadvantages. Richards (1981), compared the physiological responses of the deciduous treeline species, Larix lyallii, with the sympatric evergreen conifers, Abies lasiocarpa and Picea engelmannii. The lack of leaves and the isolation of buds from the xylem during winter give alpine larch a greater resistance and tolerance to winter desiccation than the sympatric evergreens. The summer disadvantages of deciduousness are related to the adaptations necessary to maintain a positive carbon balance. Alpine larch leaves have a high photosynthetic capacity and high diffusive conductances, but the high light compensation and saturation points restrict it to open habitats. The high leaf area to weight ratio permits a high carbon gain from a low carbon investment. Summer water use is high and photosynthesis is significantly reduced by soil and atmospheric moisture stress. He concludes that deciduous trees may have an advantage over evergreens in treeline areas where summer precipitation is high and regular and severely desiccating conditions occur during winter. As with evergreen species, summer conditions affect shoot growth and maturation of deciduous trees and increase the susceptibility to winter and spring desiccation damage at higher elevations. Thus, the general treeline model for evergreens is also applicable to deciduous species.

An interesting feature of Larix lyallii is that young trees (<20-25 yr) maintain a substantial committment to wintergreen needles during the critical period of plant establishment and root system development (Richards 1981). The wintergreen needles appear to be less susceptible to drought stress in the summer and are usually protected from desiccation by snow cover in the winter. They provide the young trees a summer advantage with no winter disadvantage. The change to deciduous needles occurs when rapid height growth projects the trees above the winter snowpack. A high photosynthetic capacity during summer and a resistance or tolerance to desiccation during winter become increasingly important. This change in the importance of needle types in alpine larch emphasizes the relative advantages of the deciduous versus evergreen habits and the importance of winter snow cover to protect evergreen leaves from winter desiccation for trees at treeline.

B. Shrub Vegetation at Treeline

Shrubs are a major component of the vegetation at treeline and in the alpine and low arctic tundra in the Northern Hemisphere. Deciduous tall shrubs, primarily species of *Alnus* and *Salix*, are locally important at the northern treeline but are usually restricted to warmer slopes along river valleys and alluvial deposits where the active layer depths are greater than the adjacent upland tundra (Bliss and Cantlon 1957). Deciduous low shrubs are widely distributed in many treeline areas. *Salix* spp. are common in many mid-latitude mountain ranges, typically occurring on mesic sites and in cirque basins (Bliss 1975).

At higher latitudes, Betula spp. increase in importance, and this growth form becomes a dominant feature of the vegetation on mesic and upland sites where snow accumulations are greater than plant heights. Low shrubs are increasingly restricted in distribution and importance in the more severe environments at higher elevations and in the High Arctic. Dwarf shrubs characterize the shrub tundra and often form an understory to the low shrub species. These dwarf shrubs are primarily heaths (Ericaceae, Empetraceae, and Diapensiaceae) and evergreen (Cassiope spp., Ledum spp., Loiseleuria procumbens, Phyllodoce spp., Rhododendron spp., Vaccinium vitis-idaea, Empetrum spp., Diapensia lapponica), although deciduous species (Vaccinium spp., Arctostaphylos spp.) are also present. Some evergreen heaths (Empetrum spp., Loiseleuria procumbens), evergreen non-heaths (Dryas spp.), and deciduous non-heath species (Salix spp.) may occur as prostrate or cushion-like shrubs in wind exposed sites at higher elevations and in the High Arctic. However, typical habitats of the evergreen dwarf shrub heaths are snow covered in winter and nutrient poor. Heathland communities are important in many mountain areas and the Low Arctic, but are minor in the High Arctic (Bliss 1979).

Dwarf shrub heath vegetation with a high structural and floristic similarity and often with Cassiope as a major component or dominant is widespread. Evergreen and deciduous shrubs are part of the hyparctic flora (Yurtsev 1972) that evolved during the Pliocene from the alpine tundra of northeastern Asia. From this center of distribution, these species spread into "Beringia" (Hultén 1937), the Low Arctic, and many subalpine areas at high latitudes. Heathland communities occur in northern and eastern Asia (Tolmachev 1966), the European Alps (Schröeter 1926, Braun-Blanquet 1954), Scandinavia (Muller 1952, Dahl 1956, Gjaerovoll 1956), Iceland (Falk 1940), and Greenland (Oosting 1948, Böcher 1954, 1959). In North America this vegetation occurs in the Canadian arctic islands (Polunin 1948), arctic mainland Canada (Corns 1974), arctic Alaska (Hanson 1953, Britton 1957, Johnson et al. 1966), the Presidential Range of New Hampshire (Bliss 1963), and widely in the northwestern United States and Canada.

Most investigations of treeline vegetation in the Pacific Northwest are synecological having concentrated on plant community descriptions. Many of these studies include mention of dwarf shrub heath vegetation. Historical notes are provided by Rydberg (1914a,b), Harshberger (1929), McAvoy (1931), and Daubenmire (1943). More recent studies have been conducted in the Cascade Mountains of Oregon and Washington by Van Vechten (1960), Franklin et al. (1971), and Edwards (1980). Douglas (1972) and Douglas and Bliss (1977) described plant communities in the subalpine and alpine zones of the North Cascades. They stated that the Cassiope-Phyllodoce community is the most widespread community in this area. Community descriptions in British Columbia are provided by Brink (1959, 1964). Here the heath community was described as moderately chionophilous (Brooke et al. 1970) and was designated the zonal community in the alpine (Archer 1963). Similar heath shrub communities are found in the north central Olympic Mountains (Kuramoto and Bliss 1970, Olmsted 1975). Dry summers in these mountains restrict the heath communities to cool habitats with deep, long lasting snow cover such as north-facing cirque basins.

Few ecological studies have been conducted in the interior mountain ranges of British Columbia, and the descriptions of heath vegetation are less detailed. McLean (1970) noted the importance of Phyllodoce in the subalpine forests of southern British Columbia and indicated that in the alpine zone, Cassiope mertensiana is restricted to occasional small pockets with increased moisture. Eady (1971) described similar treeline vegetation from the Big White Mountains but Cassiope was absent from the area. However, Welsh (1971) noted that both Cassiope mertensiana and Cassiope tetragona were present in northern British Columbia.

Early descriptions of treeline vegetation in the Canadian Rockies are provided by Heusser (1956) and Porsild (1959). Recent studies in more southern areas include those of Bryant (1968), Bryant and Scheinberg (1970), Trottier (1972), Baig (1972), and Kuchar (1973) in southern Alberta, and Choate and Habeck (1967) and Bamberg and Major (1968) in adjacent areas in northern Montana. Associations dominated by either Cassiope or Phyllodoce have been described in

Banff National Park by Beder (1967), Broad (1973), and Knapik *et al*. (1973). Studies in Jasper National Park and vicinity include those of Kuchar (1972a,b, 1975), La Roi *et al*. (1975), Crack (1977), Hrapko and La Roi (1978), Mortimer (1978), Wells *et al*. (1978), Lee and La Roi (1979a,b), See and Bliss (1980), and Hamilton (1981). Two different heath communities are usually recognized in these mountains, one dominated by *C. mertensiana* and *Phyllodoce*, and one dominated by *C. tetragona*. Both Kuchar (1975) and Hrapko and La Roi (1978) separated these communities on the basis of observations of exposure, time of snowmelt, and soil moisture.

C. Adaptive Strategies of Dwarf Shrubs at Treeline

Evergreen and deciduous dwarf shrubs possess contrasting whole plant strategies of adaptation to tundra environments. They are characterized by differences in carbon and nutrient allocation which may have functional importance associated with particular habitats (Bliss 1962). Both growth forms have species distributed widely over mesotopographic gradients, and some in exposed sites have evolved the cushion habit. Disregarding the latter, some habitat generalizations can be made. Both generally occur in sites that are snow covered in winter. Evergreen dwarf shrubs tend to characterize sites that are nutrient poor or where water stress develops during the growing season. Deciduous dwarf shrubs do not show as distinct habitat preferences and tend to decrease with altitude and latitude (Tieszen and Wieland 1975, Bliss 1979). The characteristics of these two growth forms will be briefly discussed with emphasis on the evergreen habit and its success in dwarf shrubs at treeline.

Dwarf shrubs, as with most tundra plants, tend to be long-lived. This condition is favored in severe tundra environments with short growing seasons, but is a requisite in plants which make a substantial investment in structural tissue. Plant longevity may be 30-50 yr or more, but yearly shoot growth is limited (1-3 cm/yr). Rates of shoot growth tend to be higher in deciduous species (Bliss 1963). The energy efficiency of shoot production of heath communities may be high (Bliss 1963). Both deciduous and evergreen dwarf shrubs compartmentalize 80-90% of current above ground biomass in leaves and 10-15% in stems (Johnson and Tieszen 1976). Leaf expansion occurs rapidly in deciduous species and senescence in the fall results in a definite seasonality of radiation interception by the canopy. Evergreen species may also display a rapid leaf expansion phase, but full leaf development is often not reached until near the end of the growing season. Functional evergreen leaves are retained for 2-5 yr or more, allowing a long period of radiation interception, particularly in the early season when soil moisture is not limiting. The evergreen habit may be a general adaptation to shortened growing seasons caused by late snow release or late season water stress (Tieszen and

Wieland 1975). Net annual production of heath communities is often high which appears anomalous considering the slow growth rates of the plants. Production rates of alpine (Bliss 1963) and arctic (Bliss 1979) heath communities are some of the highest reported for tundra plant communities.

Sexual reproduction, which requires considerable heat input for fruit maturation and seed set, may be limited in the energy-poor tundra environments (Bliss 1971). Dwarf shrubs, particularly the evergreen heaths, flower extensively each year and produce large quantities of small seeds, although viability may be reduced. Seed germination rates of dwarf shrubs are highly variable and are often low for heath species (Nichols 1934, Bliss 1958, Karlin 1978). Heath seedlings are often extremely small and have low growth rates. Successful seedling establishment occurs infrequently and may be substrate limited in the dwarf shrub communities (Karlin 1978, Edwards 1980). The low carbon investment in reproductive parts (5%) in tundra shrubs may reflect the importance of vegetative reproduction in these species (Johnson and Tieszen 1976). Most dwarf shrub species produce long-lived rhizomes or root adventituously from decumbent shoots (Bliss 1956), and such vegetative reproduction maintains most local populations.

The photosynthetic capacity of tundra species of different growth forms appears to be inversely related to leaf longevity (Johnson and Tieszen 1976). Evergreen dwarf shrubs characteristically have low rates of photosynthesis

(1-10 mg CO_2•g dry wt^{-1}•h^{-1}) which are offset by extended leaf longevity. Conversely, deciduous dwarf shrubs have high fixation rates (10-40 mg CO_2•g dry wt^{-1}•h^{-1}) and relatively short leaf longevity (Hadley and Bliss 1964, Small 1972b, Tieszen and Wieland 1975, Johnson and Tieszen 1976). Maximum photosynthetic capacities are usually reached in current or one year old leaves of evergreen dwarf shrubs and are generally lower, although sometimes constant, in older leaves (Hadley and Bliss 1964, Grace and Woolhouse 1970, Johnson and Tieszen 1976). The lower rates of carbon dioxide uptake in evergreen versus deciduous dwarf shrubs is in part due to the lower maximum leaf conductances (higher leaf resistances) of these species (Körner *et al*. 1979, Oberbauer and Miller 1981). This results in lower rates of water uptake and transpiration (Pisek and Cartellieri 1934, Bliss 1960) and may be an adaptation to water stress (Courtin and Mayo 1975).

The evergreen dwarf shrubs typically possess small, sclerophyllous leaves with a number of xeromorphic features that may include a thickened cuticle, sunken or protected stomata, or a thick tomentum. These features contribute to many of the conservative characteristics of these plants such as the low CO_2 conductances and photosynthetic rates, but they may extend the photosynthetic period in seasonally-water stressed habitats. Evergreen heath species frequently experience low leaf water potentials (Small 1972c, Oberbauer and Miller 1981) and leaf sclerophylly may provide the cell strengthening necessary to withstand low water contents and maintain a positive carbon balance under water stress. The increased cutinization and lignification and high fiber to protein ratio may be modifications necessary to provide structural strength for overwintering leaves (Small 1972b) or a resistance to winter desiccation (Gates 1914). Many subalpine and subarctic heathlands may also experience seasonal waterlogging (Specht 1981b) and the natural xeromorphy of these plants may contribute towards a tolerance of conditions in the rhizosphere (Armstrong 1981) unrelated to water stress (Small 1972c, Marchand 1975).

Heathland habitats, both wet and dry, are characterized globally by acidic, infertile soils (Specht 1981a). In tundra environments, low soil temperatures influence nutrient cycling rates and result in low available nitrogen and phosphorus which may limit production (Haag 1974). Evergreen dwarf shrubs have low levels of these elements in their foliage and the evergreen, sclerophyllous habit may represent a mechanism for nutrient accumulation and conservation (Small 1972a). Low rates of protein synthesis and storage (Hadley and Bliss 1964) favors the production of structural tissue (xeromorphic features), making the low photosynthetic rates comparatively more efficient in the use of acquired elements, particularly nitrogen, in nutrient-deficient environmments (Small 1972b, Haag 1974).

The evergreen, sclerophyllous habit represents the minimum energy cost of drought adaptation and nutrient conservation (Mooney 1974). The high energy costs of evergreen leaves related to year around maintenance and perhaps the synthesis of compounds involving predator and overwintering protection (Johnson and Tieszen 1976) are offset by a more efficient utilization of limited nutrient elements and of a shortened growing season caused by late snow release, seasonal water stress, or waterlogging. Thus, many of the conservative characteristics of the evergreen dwarf shrubs at treeline derive from features enabling the plants to maintain the evergreen habit. The adaptive strategies of this growth form allows efficient utilization of treeline environments. However, the advantages related to evergreeness can only be realized if leaf longevity is maintained which generally requires the protection afforded by winter snow cover in severe tundra environments.

D. Cassiope

The genus Cassiope D. Don is a member of the family Ericaceae that includes some 100 genera and 3000 species occurring on all continents except Antarctica. The relationships between Cassiope and the other members of the family have been uncertain due to the diversity of the Ericaceae (Hooker 1876, Drude 1897, Good 1926, Watson et al. 1967) and the morphological and anatomical similarities of Cassiope and Calluna vulgaris Salisb. (Watson 1964, Stevens 1970). Cassiope, and the closely related genus Harrimanella Coville, have recently been placed in the tribe Cassiopeae

Stevens within the subfamily Vaccinioideae Endl. (Stevens 1971).

Cassiope is a small genus of seven (Watson 1964) to no more than twelve (Szczawinski 1962) species with its center of distribution in the Himalayas and northeastern Asia (Stevens 1970). It is a component of the hyparctic flora that evolved in part from the "gol'tsy" (alpine tundra) during the Pliocene. Most species are restricted to Asia or are amphi-beringian where they are found at alpine treeline. Cassiope ericoides (Pall.) D. Don barely extends into the Low Arctic in northeastern Asia (Tolmachev and Yurtsev 1980), and C. tetragona (L.) D. Don is widespread circumpolar in the Low Arctic and extends into the High Arctic in North America.

Four major taxa of Cassiope are recognized in North America. The following species descriptions and geographic distributions derive from a number of sources including Moss (1959), Szczawinski (1962), Wiggins and Thomas (1962), Porsild (1964), Hultén (1968), Munz and Keck (1973), Welsh (1974), and Porsild (1980). Cassiope stelleriana (Pall.) DC extends from Japan and eastern Siberia along the coast of Alaska and British Columbia to northern Washington (Mount Rainier). It differs morphologically from the other North American taxa by having adaxially flat, alternate, spreading leaves and terminal flowers on short pedicels. Cassiope lycopodioides (Pall.) D. Don is also found in eastern Asia, and in North America extends from the Aleutian Islands to southeast Alaska and northern British Columbia. Both of these species are found at treeline but they are not widespread or locally abundant. *Cassiope lycopodioides* closely resembles *C. mertensiana* (Bong.) D. Don but has smaller (1.5-3 mm), pubescent leaves with scarious margins. *Cassiope mertensiana*, a North American endemic, is found from southern Alaska and the Yukon, south to central California, and east to Idaho and Montana. Two forms are recognized; subsp. *mertensiana* has puberulent stems and pedicels, entire calyx lobes, and glabrous leaves, while subsp. *gracilis* has glabrous stems and pedicels, and minutely-ciliate leaves. Some intermediate forms do occur and it is often impossible to separate subspecies by these characters (Szczawinski 1962). Some specimens have thin, scarious leaf margins that suggest genetic interchange with *C. lycopodioides* (Welsh 1974). *Cassiope tetragona* is the most widely distributed taxon in the genus. In North America it is found in scattered localities in the High Arctic (to north of 83°N in Greenland), is widespread in the Low Arctic, and extends south in the interior ranges of the Rocky Mountains to Montana. It is separated from the other taxa by the presence of a distinct, abaxial leaf groove. Two morphologically recognizable forms occur; subsp. *tetragona* is more common in the north, and subsp. *saximontana* is a weakly differentiated Rocky Mountain form with smaller flowers and shorter pedicels. *Cassiope tetragona* is biochemically (flavonoids) distinct from the other North

American taxa, but the two subspecies are not clearly different (Denford and Karas 1975). Cassiope tetragona may hybridize with C. ericoides in Asia (Tolmachev and Yurtsev 1980), but no hybrids have been reported in North America. However, this author has observed plants with characters intermediate between C. tetragona and C. mertensiana but they are not common and their taxonomic status is uncertain.

Cassiope tetragona and C. mertensiana, the two most common species in North America, are similar in their growth habit (Fig. 1). Both are evergreen, dwarf shrubs (0.5-3 dm high) with numerous rhizome or stolon-like stems tufted on a thick base, and with ascending branches in C. mertensiana and somewhat coarser, ascending to erect branches in C tetragona. Both species have small, leptophyllous (Raunkaier 1934) leaves, imbricated in four rows and long-persistent after dying. Leaves are sclerophyllous, with a thickened cuticle and xeromorphic features. Leaf morphology and anatomy are the most obvious characters that separate these two species. Leaf shapes are basically similar and of the "Calluna" type, i.e. stalkless, sagittate with tails around the stem, and closely imbricated. Cassiope tetragona, as noted, has a conspicuous furrow down the abaxial surface of the leaf. Palisade tissue orientation is reversed in both species and occurs on the abaxial surface. The mesophyll layer in C. tetragona is spongy and filled with many air spaces. Cassiope mertensiana leaves are glabrous to minutely-ciliate, but C. tetragona leaves are densely

Figure 1. Cassiope mertensiana (a) and C. tetragona (b) habit. Dryas octopetala is visible in the foreground of b. Photographs taken in August, 1975 (a) and July, 1976 (b).

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glandular on the adaxial surface (with a few trichomes) and in the abaxial groove (with many trichomes). Stomates occur in a broad band down the center of the adaxial leaf surface in C. mertensiana. Stomates of C. tetragona occur in a few rows (ca. 5) down the center of the adaxial surface and are abundant in the abaxial groove. Leaves of C. mertensiana frequently project at a slight angle away from the stem exposing the stomates, whereas leaves of C. tetragona are more closely imbricated and the stomates more protected.

Floral characteristics are very similar in the two species. Flowers are solitary, arising from axillary buds, the pedicels longer than the subtending leaves; sepals 2-2.5 mm long, whitish (C. tetragona) or 2-3 mm long, scarious margined, whitish to pinkish (C. mertensiana); corrola open-campanulate with prominant lobes, whitish, 4-6 mm long (C. tetragona subsp. saximontana) or 6-8 mm long (C. mertensiana); stamens 8 or 10, included; anthers awned, opening by terminal pores; ovary 4-5 celled; style 1, persistent; stigma small; capsule spherical to ovoid, loculicidally 4-5 valved; seeds small and numerous.

E. Objectives

Cassiope mertensiana and C. tetragona, as has been noted, are major components of the treeline and alpine vegetation in the Pacific Northwest, but each species gains dominance in different geographic areas (Fig. 2). Cassiope mertensiana is abundant in maritime regions but is

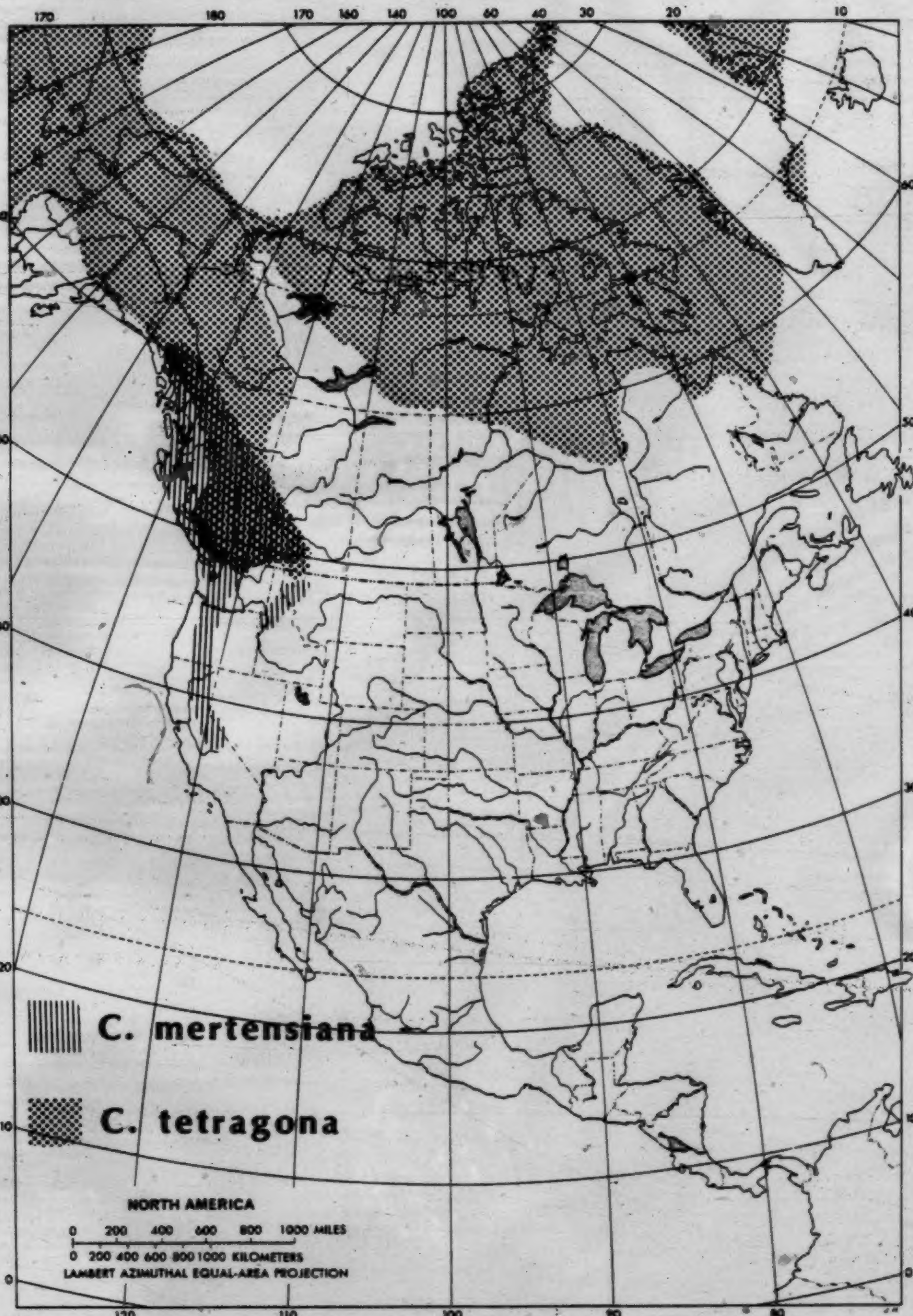
C. mertensiana
C. tetragona
NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80

Figure 2. Range distribution map of *Cassiope mertensiana* and *C. tetragona* in North America. See text for sources.

restricted to lower elevations or more protected sites in the drier mountain ranges to the east. In the Cordilleras, C. tetragona is restricted to these drier interior ranges. The species are sympatric in the Alberta Rocky Mountains but are separated along the complex gradient of exposure near treeline. Here, C. mertensiana is more common in the upper subalpine and occurs above treeline only in protected sites. Casiope tetragona often occurs in exposed sites in the upper subalpine, but is more common in the low alpine zone. This study examines the factors that influence the distribution of these two species near treeline in the Canadian Rocky Mountains. The main question is why C. mertensiana is primarily a subalpine species whereas C. tetragona is primarily an alpine species. The emphasis is on the factors that limit C. mertensiana at higher elevations and prohibit it from occupying the more exposed C. tetragona sites. The objectives of the study are to:

1. Provide quantitative data for microenvironmental comparisons of habitats occupied by C. mertensiana and C. tetragona in the upper subalpine and alpine zone.
2. Compare the physiological responses and adaptations of the two species that determine their niche separation.

Studies of evergreen dwarf shrub heaths at alpine treeline in the European Alps (Larcher 1957, Tranquillini 1963, Caldwell 1970) and in western North American Mountains (Olmsted 1975, Edwards 1980) suggest that a wide range of environmental factors and plant adaptations influence their success at treeline. These include a difference in tolerance to seasonal atmospheric and soil moisture stress during the summer and low temperatures or desiccation during the winter. From these studies and observations of Kuchar (1975) and Hrapko and La Roi (1978), the following hypotheses were developed to explain the niche separation of _C_. _mertensiana_ and _C_. _tetragona_:

a. _C_. _mertensiana_ is unable to tolerate low air temperatures during fall and winter in exposed microsites and thus avoids these conditions under a deep snow cover.

b. _C_. _mertensiana_ is unable to tolerate winter desiccation in exposed microsites.

c. _C_. _mertensiana_ is unable to tolerate late summer drought, and is therefore restricted to late meltout microsites with a more favorable soil moisture regime.

d. _C_. _tetragona_ is unable to withstand shortened growing periods in late meltout microsites.

A study of the limitations to growth of these two species will aid in understanding the patterning of vegetation near treeline in the Canadian Rocky Mountains and perhaps help explain the geographic distribution of the species in the Cordilleras of North America. However, this study has broader implications. Most species of _Cassiope_, as well as most of the evergreen dwarf shrub heaths at treeline, occupy upper subalpine habitats similar to those of C. mertensiana. Cassiope tetragona is the only member of this genus, and one of the few of this growth form, that is truly characteristic of tundra (alpine or arctic) environments. The above cited studies of treeline heaths were conducted on a wide range of genera possessing diverse gross morphologies and xeromorphic features. Also, they have dealt primarily with upper subalpine species and habitats, and neither Cassiope nor alpine heaths have been intensively studied. In contrast, this study focuses on factors limiting to C. mertensiana and C. tetragona. The results should suggest environmental and physiological constraints to growth of this life form in severe tundra environments at higher elevations and latitudes.

II. STUDY AREA DESCRIPTION

A. Location

Signal Mountain (latitude 52° 51' N, longitude 117° 59' W) in Jasper National Park, Alberta, was selected as the research area (Figs. 3 and 4). The 2 km summit ridge is 2255 to 2311 m above mean sea level and is located approximately 8 km east of Jasper townsite at the extreme NW end of the Maligne Range, the easternmost of the Main Ranges of the Rocky Mountains in this region. Signal was selected as the research area because 1) both *C. mertensiana* and *C. tetragona* are abundant on the mountain in habitats typical of large areas in the Canadian Rockies, 2) the long (500 m plus) NE alpine slope provides a gradual gradation in microenvironments and plant communities from exposed sites along the summit ridge to protected sites near treeline, 3) other researchers have described the flora and many of the plant communities of the alpine zone (La Roi *et al*. 1975; Hrapko and La Roi 1978; Lee and La Roi 1979a,b), and 4) the alpine zone is accessible in summer (car) and winter (snowmobile, snowshoes or skis) *via* a 9 km fire lookout access road. Winter access to the alpine zone, possible in only a few areas in the Canadian Rockies, was a prime consideration.

Two study sites were selected on the north slope of Signal Mountain (Figs. 5 and 6). Intensive study Site 1 (2060 m) was located in a *C. mertensiana* community on a

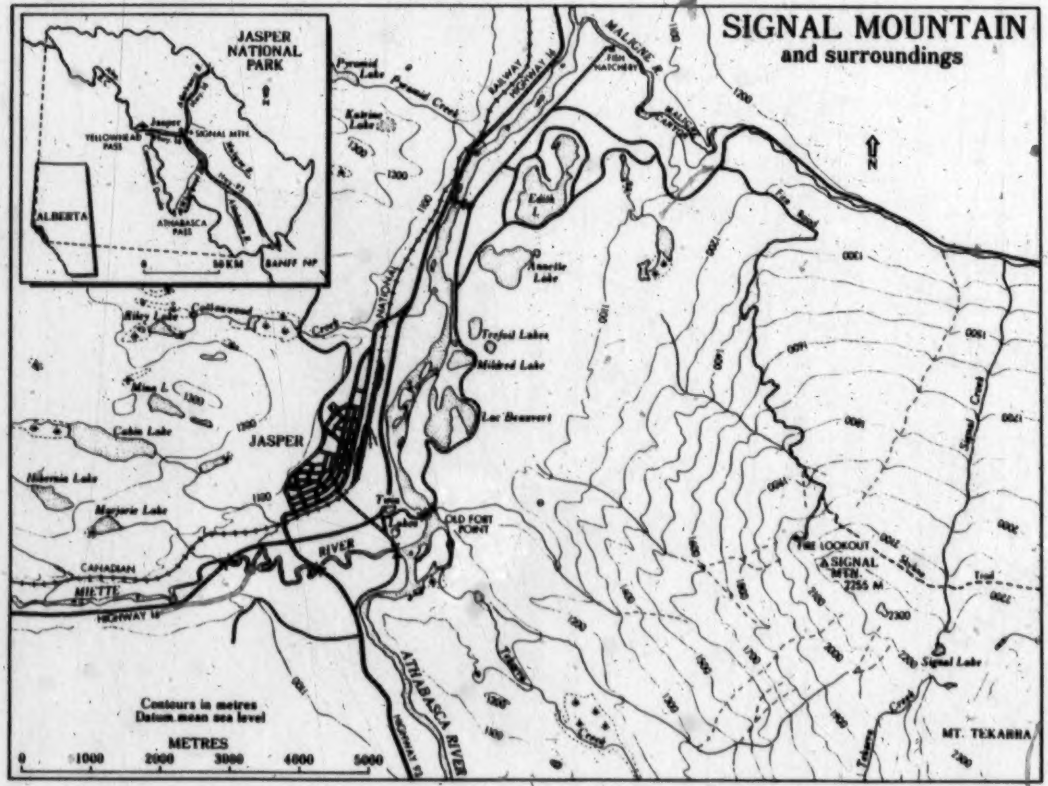
SIGNAL MOUNTAIN
and surroundings
N
JASPER NATIONAL PARK
ALBERTA
YELLOWHEAD PASS
Jasper
SIGNAL MTN.
ATHABASCA PASS
50 KM
BANFF NP
Pyramid Lake
Pyramid Creek
Katrine Lake
MALIGNE R.
FISH HATCHERY
RAILWAY
HIGHWAY 16
Edith L.
Annette Lake
Trefoil Lakes
Mildred Lake
Lac Beauvert
Riley Lake
Cottonwood
Creek
Mina L.
Cabin Lake
Hibernia Lake
Marjorie Lake
JASPER
NATIONAL
CANADIAN
MIETTE
RIVER
OLD FORT POINT
ATHABASCA RIVER
HIGHWAY 93
Fire Road
FIRE LOOKOUT
SIGNAL MTN. 2255 M
Trail
Signal Creek
Signal Lake
MT. TEKARRA
Tekarra Creek
Contours in metres
Datum mean sea level
METRES
0
1000
2000
3000
4000
5000

Figure 3. Location of Signal Mountain and Jasper National Park, Alberta, Canada. From Hrapko and La Roi (1978) with permission.

Figure 4. Signal Mountain (S) and the Maligne Range in winter. Study sites were located along the NE slope (in shadow), from treeline to the summit ridge. The Athabasca River Valley is in the foreground and Jasper townsite at lower right. Photograph taken from the summit of Pyramid Mountain, 14 km to the NW of Signal, on December 22, 1974.

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Figure 5. Two views of the upper subalpine Site 1.

a. View downslope (to north) across the C. mertensiana community. Cassiope tetragona occurs upslope of the photograph site. Photograph taken on July 24, 1973.

b. View downslope along the transect in winter. Shoots of C. tetragona are visible in the foreground projecting above the 12 cm snowpack; snow depth at the C. mertensiana stake (arrow) is 50 cm. Photograph taken on December 21, 1974 during an early winter with light snowfalls.

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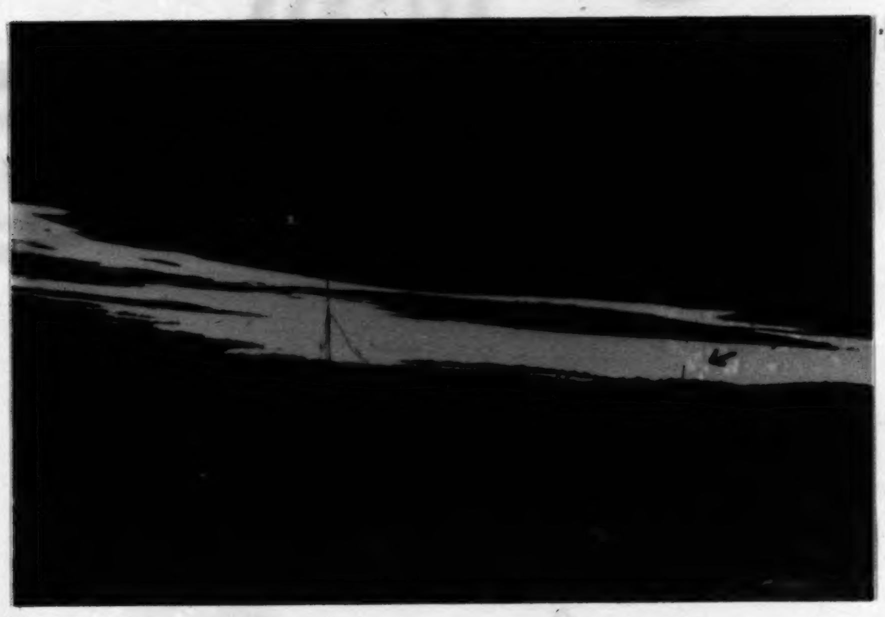

Figure 6. Two views of the low alpine Site 2.

a. The upslope end of the transect showing the transition from Dryas-Lichen (on the exposed bench to left) to C. tetragona-Dryas (downslope to right). Photograph taken on October 27, 1974.

b. View downslope along the transect. The C. tetragona-Dryas community is nearly snow free; snow depth at the C. mertensiana stake (arrow) is 180 cm. Photograph taken on June 25, 1974.

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protected slope (32%) with a north aspect (4°). Intensive study Site 2 (2195 m) was located in a C. tetragona community, also on a protected slope (30%) with a north aspect (27°), but at a higher elevation where conditions are presumably more severe. Cassiope tetragona was present at Site 1 in peripheral exposed microsites and C. mertensiana was present at Site 2 in small snow accumulation areas.

In this study, the upper subalpine zone is defined as that area above the continuous forest line but below treeline (krummholz with supranival leaders), and the alpine zone is that area above treeline and may include scattered krummholz. On the north slope of Signal Mountain the continuous forest line is at 2015 m and treeline is at 2090 m. Study Sites 1 and 2 are located in the upper subalpine and low alpine zones, respectively.

B. Geology, Glacial History and Geomorphology

The Eastern Cordillera of the Canadian Rocky Mountains has been subjected to two orogenies. The Cariboo Orogeny (early Devonian) had the most effect on strata west of the Rocky Mountain Trench and probably resulted in broad folding with only very minor intrusions in the Eastern Cordillera. The major structural features in the east derive from the Rocky Mountain (Laramide) Orogeny, accurately dated as Eocene. Compression forces from the west caused folding of sedimentary rocks and faulting, with little or no instrusion (McCrosson and Glaister 1964). A series of imbricate thrust sheets has resulted in separate parallel mountain ranges and major valleys oriented in a general northwest to southeast direction, parallel to the major faults and strike of the rock (Roed 1964). The many faults are relatively closely spaced in the Foothills and Front Ranges but are more widely spaced under the Main Ranges. The main thrust fault in the Jasper region is the Pyramid Thrust, a low angle fault which parallels the northeast slope of Signal Mountain near the Maligne River and bounds the Main Ranges on the east (Charlesworth _et_ _al_. 1967). The Puget or Cascadian Orogeny (Miocene-Pliocene) primarily effected the Western Cordilleras.

Subsequent erosion has exposed strata of Paleozoic and Mesozoic age in the Foothills and Front Ranges and Precambrian to Mississippian age in the Main Ranges. The bedrock of Signal Mountain belongs to the Precambrian Miette Group whose beds crop out over a wide area of the Maligne Range and form low, rounded mountain ridges due to their generally recessive nature (Roed 1964). Rocks of the Old Fort Point Formation, consisting mainly of slates and siltstones, crop out at the Name Site on the southwest slopes of Signal. Overlying these are poorly sorted arenaceous and argillaceous sedimentary rocks of the Lower Member of the Wynd Formation. The ridge-forming arenaceous units, primarily sandstones and conglomerates, crop out along the summit ridge. These are interbedded with recessive argillaceous beds of slate and siltstone, the weathering of which has resulted in several elongated troughs and benches on the north slope of Signal, nearly parallel with the summit ridge. Relatively protected slopes along these benches are vegetated by plant communities dominated by C. tetragona and C. mertensiana at high and low elevations, respectively. Conglomerates and sandstones of the Upper Member of the Wynd Formation and the Jasper Formation crop out on adjacent slopes of Tekarra Mountain, east of Signal. Quartzites of the Lower Cambrian Gog Formation overlie the Miette strata and form spectacular cliffs on the upper slopes of Tekarra.

The Canadian Rocky Mountains were repeatedly occupied by valley and piedmont glaciers during the Pleistocene. Pre-Wisconsin Cordilleran glaciers occurred in the Athabasca Valley area as evidenced by glacial erratics at high elevations east of the limits associated with the Wisconsin Cordilleran tills (Bayrock and Reimchen 1975, Roed 1975). Wagner (1966) has tentatively correlated the Lower Mountain Till from Southwestern Alberta as Illinoian and Shaw (1972) suggests these older advances may be synchronous. Roed (1975) has differentiated four Cordilleran tills in the Hinton-Edson area east of Jasper. Glacial erratics associated with the Marlboro Till, which probably represents the Early Stage of the Pinedale or Classical Wisconsin Glaciation of the Rocky Mountain area of the United States, suggest ice at elevations sufficient to cover Signal Mountain. Metamorphic erratics of the Athabasca Valley

Erratics Train were deposited near Edson at elevations of 1585 m by a glacier originating in the northern part of the Monashee Mountains and Premier Range of British Columbia and crossing the Continental Divide near Jasper (Roed et al. 1967). Quartzitic rocks derived from the Gog Formation were deposited as the Foothills Erratic Train along the foothills of Alberta and into Montana by a later coalescence of the Marlboro (Cordilleran) and Edson (Laurentide) Glaciers (Reeves 1973). The subsequent Obed and Drystone Creek Glaciers (Middle and Late Pinedale) also deposited till in the lower foothills east of Jasper (Roed 1975). Signal Mountain was buried by this Wisconsin ice as evidenced by scoured bedrock and roches moutonnées on the summit ridge and glacial drift and erratics on the slopes. The Athabasca Valley near Jasper was ice-free by 10,550 yr B.P. (Reeves 1973).

Periglacial and recent cryopedogenic activity on Signal Mountain has resulted in many types of patterned ground (Washburn 1956, 1973; Johnson and Billings 1962). Stone and vegetation stripes are common on southerly exposures and sorted and nonsorted circles, nets, steps, and solifluction terraces are abundant on the northerly lee slopes. Snow accumulation produces many late-melting and one permanent snow-field which supply adequate moisture for the maintenance of these latter features. Nonsorted stepped frost boils are common in the C. tetragona communities and are active as evidenced by organic matter incorporation into the soil profiles and patterns of root and shoot growth. Most of these steps are completely vegetated but many areas of bare soil are sufficiently disturbed by spring and fall needle ice activity to prevent plant colonization. Greater snow accumulation and soil moisture in the _C_. _mertensiana_ communities produces more prominant nonsorted circles and nets. These grade from small stepped frost boils (vegetated) to larger frost hummocks, depending on topography and water supply. Current activity of these features is also indicated by patterns of organic matter incorporation and root growth. Ice and frozen soil were observed at 50 cm depth below some of these hummocks in early August. Permafrost probably only exists below the larger peat hummocks of the alpine bogs surrounding meltwater ponds and below the larger solifluction terraces.

C. Vegetation

The vegetation of Jasper National Park is well documented (Wells _et_ _al_. 1978). Based upon vegetation and floristics, Jasper lies near the boundary between the Northern and Far Northern Rocky Mountain Divisions of Daubenmire (1943) and within the Northern Alberta Rocky Mountain region of Ogilvie (1962). Three major vegetation zones are recognized along an elevation gradient in the study area (Moss 1955, Rowe 1972, La Roi _et_ _al_. 1975): montane (1000-1500 m), subalpine (1500-2100 m), and alpine (>2100m). Vegetation studies have been conducted in all three zones on Signal Mountain.

The montane zone has been characterized by the association of Pseudotsuga menziesii and Pinus contorta (Rowe 1972) and reaches its northern-most limit in the eastern Rocky Mountains in the Jasper area. This climax forest type occurs on warm, dry sites with south or west aspects in the Athabasca River valley (Stringer and La Roi 1970) and often grades into savanna and Koeleria cristata-Calamagrostis montanensis grassland on dry valley flats (Stringer 1973). The most extensive montane forest type in the area is dominated by Pinus contorta (La Roi and Hnatiuk 1980). This type occurs throughout on all slopes and valleys, often in dense even-aged stands. It extends into the subalpine, even to treeline, where fires have occurred. Pinus contorta may be a physiographic climax on some xeric sites, but is fire subclimax on most sites. It is successional in the montane to Pseudotsuga menziesii on dry sites and Picea glauca climax on mesic sites (La Roi et al. 1975). This latter type is not extensive in the area and is restricted to riparian habitats or northerly aspects (Stringer and La Roi 1970). The wide-ranging boreal species, Picea mariana, is a minor component of these montane forests, occurring on wet sites such as fens and peatlands or along stream courses (Laidlaw 1971). It is also common on poorly drained sites within the subalpine (Hettinger 1975), habitats that are quite extensive on the gentle north slope of Signal Mountain. Populus tremuloides occurs in small stands throughout the area on alluvium depositional sites, sometimes associated with Populus balsamifera (Lulman 1976). It is successional to Picea glauca on mesic sites or Pseudotsuga menziesii on xeric sites.

The dominant forest type in the subalpine zone is the widespread climax association of Picea engelmannii-Abies lasiocarpa (Biel 1966). Even-aged stands of Pinus contorta are extensive due to infrequent but intense fires under cool, mesic conditions (Tande 1979). Picea mariana occurs locally as noted, and Pinus albicaulis is often found on exposed ridges. Closed forest gives way to open Picea-Abies woodland on northerly slopes in the upper subalpine, ca. 1950-2100 m. This forest type is characterized by many age classes, vigorous Abies regeneration, and a characteristic shrub understory on hummocky microtopography composed of Cassiope mertensiana, Phyllodoce spp., and Vaccinium scoparium. Robust herbs, including Artemisia norvegica, Pedicularis bracteosa, and Arnica latifolia are also common. Study Site 1 is located near the high elevation limit of this open forest type, but with low alpine community types dominating exposed microsites between Picea-Abies tree islands.

Vegetation patterns in relation to elevation, moisture, and fire history have been well documented in the montane and subalpine zones of Signal Mountain (La Roi et al. 1975, Tande 1979, Lee and La Roi 1979a,b). Fire has been a dominant influence in the coniferous forests of the

Athabasca Valley in the Jasper vicinity, with large fires (>50% of area) occurring at a mean return interval of 66 yr. Large fires burned portions of the subalpine *Abies*-*Picea* forests on the north slope of Signal Mountain in 1889 and 1758, however, the mature climax forest near Site 1 predates the earlier burn (Tande 1979). Patterns of bryophyte and understory vascular plant species diversity on Signal Mountain are described by Lee and La Roi (1979a,b). Bryophytes have wider tolerances and habitat responses than vascular plants along the elevation gradient.

The alpine vegetation in the Alberta Rocky Mountains is dominated by dwarf shrubs including *Dryas* spp., *Salix* spp., *Cassiope* spp., and *Phyllodoce* spp. *Dryas integrifolia* dominates drier sites in the Front Ranges N of 51° latitude, whereas *D. octopetala* dominates ecologically similar areas in the Main Ranges and farther south. Heath tundra communities, possessing a high structural and compositional similarity, are widespread but increase in importance in the more mesic Main Ranges and northern regions. Graminoid species are ubiquitous but the importance of graminoid-dominated communities varies regionally. Dry, exposed site species include *Kobresia bellardii*, *Carex nardina*, *C. rupestris*, *Festuca* spp., *Agropyron latiglume*, and *Elymus innovatus*. Species of mesic, protected sites include *Carex nigricans*, *Juncus* spp., and *Luzula* spp. *Artemisia norvegica* and *Polygonum viviparum* are alpine constants. Medium shrubs, particularly *Salix barrattiana* and

Betula glandulosa, dominate wet sites and valley bottoms above treeline.

Several vegetation studies have been conducted in the alpine zone of Signal Mountain (La Roi et al. 1975, Hrapko and La Roi 1978, Lee and La Roi 1979a,b). Other studies have been conducted in the Bald Hills at the east end of the Maligne Range (Kuchar 1972a, 1975) and in other areas of Jasper National Park and vicinity (Kuchar 1972b, Crack 1977, Mortimer 1978, Wells et al. 1978, See and Bliss 1980, Hamilton 1981). The alpine flora of Signal Mountain includes 157 vascular, 57 bryophyte, and 53 lichen species (Hrapko and La Roi 1978) and is depauperate compared with adjacent areas (Mortimer 1978). The vascular flora is high in circumpolar arctic-alpine (30%), amphi-beringian (9%), and widespread cordilleran (19%) species and low in low-elevation North American (5%) species (Mortimer 1978). The alpine vegetation is "northern" in physiognomy and floristics.

A detailed description of alpine plant communities and physical habitats on Signal Mountain is provide by Hrapko and La Roi (1978), from which the following is derived. Fifteen community types, seven Dryas dominated, were delineated into four tundra groups. The vegetation in exposed sites is dominated by Dryas, and only the Dryas-Oxytropis, Dryas-Festuca, and Potentilla-Silene communities are found on the dry SW slope. Cassiope communities occur only on the leeward NE slope, which is less steep, more heavily vegetated, and with more complex vegetation patterns. The Cassiope tetragona-Dryas community is very common in slightly concave areas that are protected but not deeply buried by winter snow. Salix arctica, S. nivalis, and Artemisia norvegica are important as are fruticose lichens. The Cassiope mertensiana- Phyllodoce glanduliflora community is common in protected microsites such as topographic depressions, the bases of solifluction terraces, and at lower elevations. Artemisia norvegica is also common but graminoids and bryophytes have increased importance. Both Cassiope communities occur over large areas of alpine tundra in the Alberta Rockies, particularly in Jasper National Park and the North.

Cassiope tetragona and C. mertensiana show niche separation related to exposure, snow accumulation, time of snow melt, and soil moisture. Figure 7 shows the distribution of Cassiope and community dominants in a typical snow accumulation site (Extensive Site 4) at 2135 m, intermediate to study Sites 1 and 2. Cassiope tetragona becomes more extensive at higher elevations while C. mertensiana increases near treeline. Carex-Luzula often forms a distinct community in a zone interior to C. mertensiana in sites of greater snow accumulation. This vegetation pattern is common in the low alpine and similar profiles (often truncated due to microtopographic differences) are described by Kuchar (1975), Hrapko and La Roi (1978), and Mortimer (1978).

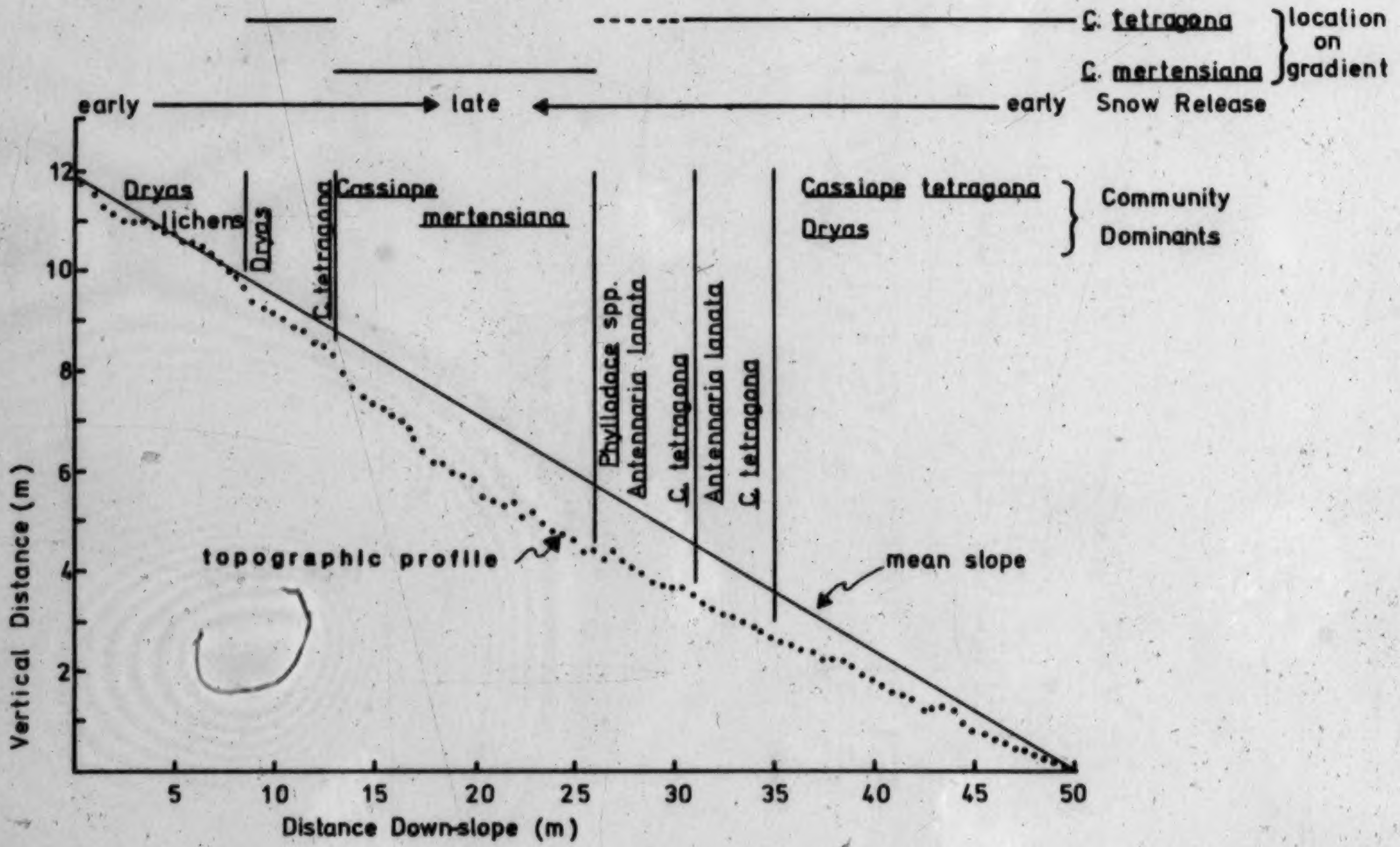


Figure 7. Topographic profile of a typical small alpine snowbed (Extensive Site 4) showing distribution of Cassiope spp. and community dominants. The species listed show distributions nearly as abrupt as indicated. Vertical exaggeration is 2.5 X.

D. Soils

Soils of the montane and subalpine zones in Jasper National Park have developed primarily on colluvial, alluvial, glacial, and aeolian parent materials. Complex geologic structure and variable lithologies, climate, and vegetation, influence pedogenesis regionally and locally. Most soils of these zones belong to the Regosolic, Brunisolic, Luvisolic, Podzolic, and Gleysolic Orders (Canada Soil Survey Committee 1978). Descriptions of soils associated with the major vegetation types are provided by Biel (1966), Stringer and La Roi (1970), Laidlaw (1971), Stringer (1973), Lulman (1976), and La Roi and Hnatiuk (1980).

Pedogenesis in the alpine zone is primarily controlled by climate (i.e. low temperature) that inhibits biological and chemical processes (Retzer 1965, 1974). Soils generally have weakly developed and often thin horizons. Soil pedons are often buried or truncated, with discontinuous horizons in areas subject to soil creep and frost action. Alpine soils are characterized by accumulations of weakly decomposed organic matter in the surface horizons, weak granular structure, silt loam textures with low clay contents, and an acid pH that increases with depth (Knapik et al. 1973). Illuvation is usually slight and the B horizon is primarily altered by oxidation producing a change in color rather than texture. Podzolization, resulting in significant amounts of amorphous aluminum and iron compounds, has been reported in geographically widespread alpine areas (Bliss and Woodwell 1965; Johnson and Cline 1965; Sneddon _et_ _al_. 1972a,b; Van Ryswyk and Okazaki 1979) including the Canadian Rocky Mountains (Baptie 1968, King and Brewster 1976). Lithic and cryic contacts often occur close to the mineral soil surface.

Alpine soils have been described from a number of locations in the Canadian Rocky Mountains including Waterton Lakes National Park (Coen _et_ _al_. 1977), Banff National Park and vicinity (Baptie 1968, Beke and Pawluk 1971, Broad 1973, Knapik _et_ _al_. 1973, King and Brewster 1976) and in Jasper National Park and vicinity (Kuchar 1975, Hrapko and La Roi 1978, Mortimer 1978, Wells _et_ _al_. 1978). Soils belonging to the Regosolic, Brunisolic, Podzolic, and Gleysolic Orders are represented. These soils have developed primarily on thin glacial till and colluvial parent materials but lacustrine deposits occur in localized depressional areas (Knapik _et_ _al_. 1973) and aeolian deposits of volcanic ash (Mazama 6600 yr B.P., St. Helens "Y" 3350 yr B.P., Bridge River Ash 2400 yr B.P.) are widespread. Podzolic B horizons common in many soils of the region, may have resulted from degradation of this ash _in_ _situ_ rather than podzolization _sensu_ _stricto_ (Beke and Pawluk 1971, King and Brewster 1976).

Soils of habitats occupied by _C_. _mertensiana_ and _C_. _tetragona_ have been described from many Alberta areas, and soil Orders include Regosols, Brunisols, and Podzols (Table

Table 1. Soil Great Groups and Subgroups found in *C. mertensiana* and *C. tetragona* habitats from selected areas of the Canadian Rocky Mountains.

LOCATION AND REFERENCE	HABITAT TYPES	
	C. mertensiana	*C. tetragona*
HIGHWOOD PASS		
Trottier 1972	Alpine Eutric & Drystric Brunisols	Orthic Regosols
	(*Phyllodoce* Association)	(*C. tetragona* Association)
BANFF NAT'L PARK		
Baptie 1968	Podzo Regosols	Podzo & Cryic Regosols
	(*Phyllodoce*-*Vaccinium* Association)	(*C. tetragona* Association)
Broad 1973	Podzols	
	Regosols	
	(*C. mertensiana* Association)	
	Brunisols	
	Podzols	
	Regosols	
	(*Phyllodoce* Association)	
Knapik *et al.* 1973	Alpine Dystric Brunisols	Alpine Dystric Brunisols
	(*Phyllodoce*-*Antennaria*)	(*C. tetragona*)
King & Brewster 1976	Orthic Humo-Ferric Podzols	Orthic Ferro-Humic Podzols
	(Subalpine-*Phyllodoce*)	(Subalpine-*Phyllodoce* & *C. tetragona*)

Table 1. (continued)

LOCATION AND REFERENCE	HABITAT TYPES	
	C. mertensiana	*C. tetragona*
JASPER NAT'L PARK VICINITY		
Kuchar 1975	Dystric Brunisols (*C. mertensiana-Phyllodoce*)	Dystric Brunisols (*Dryas-C. tetragona*)
Mortimer 1978	Orthic Melanic & Eutric Brunisols (*Phyllodoce-C. mertensiana*)	Orthic Regosols (*C. tetragona-Dryas*)
Wells *et al*. 1978	Sombric & Melanic Brunisols Sombric Humo-Ferric Podzols (*Phyllodoce-C. mertensiana*)	Sombric & Melanic Brunisols Eluviated Dystric Brunisols Orthic & Sombric Humo-Ferric Podzols (*C. tetragona-Dryas*)
Hrapko & La Roi 1978	Orthic Sombric Brunisols (*C. mertensiana-Phyllodoce*)	Orthic Sombric Brunisols (*C. tetragona-Dryas*)

1). Soils of _C_. _mertensiana_ sites generally have greater horizon development and only rarely do Regosols occur. Soils of communities dominated by _C_. _mertensiana_-_Phyllodoce_ and _C_. _tetragona_-_Dryas_ on Signal Mountain were classified as Orthic Sombric Brunisols by Hrapko and La Roi (1978). These soils had sandy loam to silty loam textures with low clay contents (3-15%). Available nutrients, including N and P, were low, but K was highest in the soils of _C_. _mertensiana_-_Phyllodoce_ communities of any examined. Field capacity (-0.03 MPa), permanent wilting point (-1.50 MPa), and available moisture were highest in the organic horizons of the NE slope soils, including those of _Cassiope_ sites.

E. Climate

Macro and Meso-climate

The macroclimate of the Cordilleran region (Hare and Thomas 1974) is dominated by the movement of high and low pressure systems within the zone of westerlies across the many parallel mountain ranges that lie nearly perpendicular to the prevailing winds. The maritime influence (moderate temperatures, winter maximum and summer minimum precipitation) decreases in the lee of successive mountain ranges. Conversely, continentality (large temperature fluctuations, summer maximum and winter minimum precipitation) increases with proximity to the prairies. This is especially true in winter when cold arctic air from large high pressure systems over the continental interior, penetrates the mountains from the east. In general, a west-east gradient exists of decreasing precipitation and increasing temperature variability (especially in winter).

The climates of the four contiguous mountain National Parks lying along the Continental Divide in British Columbia and Alberta are discussed by Janz and Storr (1977), from which much of the following is derived. Spatial variations in mesoclimates are pronounced due to topographic influences. Dry valleys are continental while a more maritime climate may exist at higher elevations. Jasper townsite has one of the most continental climates of reporting stations in the region. This is reflected in the magnitude and variability of its temperatures and precipitation. Summer temperatures are higher and annual precipitation totals lower than most mountain or foothill sites in west central Alberta. This may be influenced by a) Jasper's low elevation (at 1061 m it is one of the lowest reporting stations in the Parks), b) Jasper's northerly latitude and proximity in winter to cold, arctic air, and c) a rain shadow effect (Powell and MacIver 1976), in part derived from the presence to the west of Mt. Robson, the highest mountain along the Divide. Storm tracks during summer frequently bypass Jasper townsite on the south and move up the Athabasca River Valley (Tande 1977).

A climatic diagram for Jasper townsite is presented in Fig. 8 (see Appendix for Atmospheric Environment Service "Normals"). The macroclimate is characterized by cold and

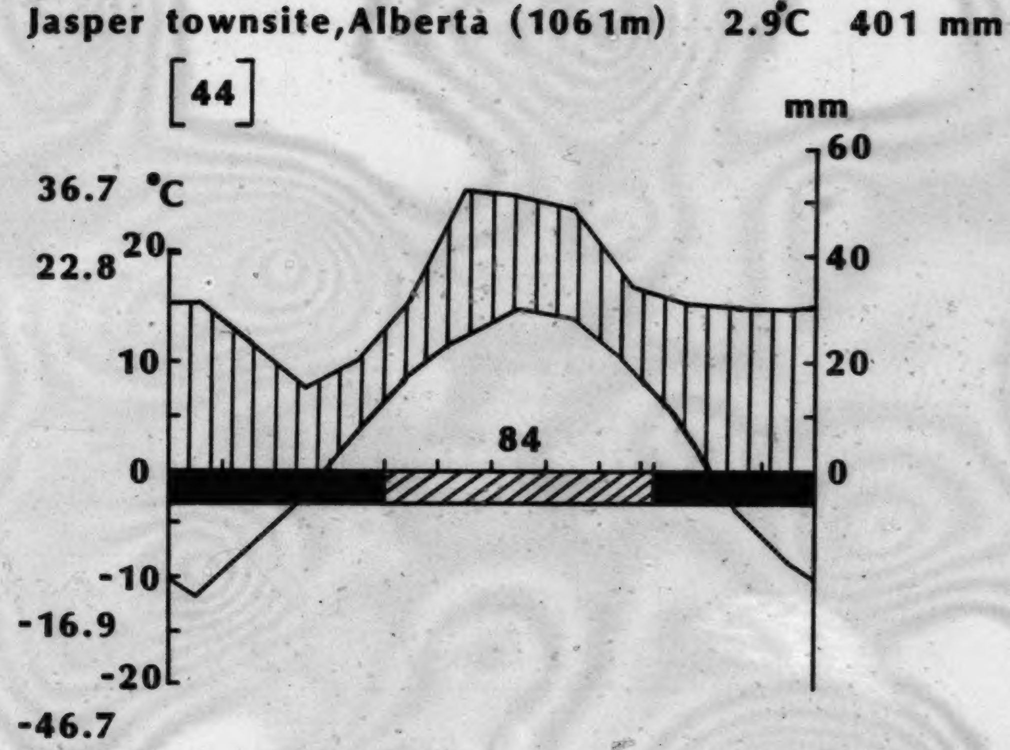


Figure 8. Climatic diagram (after Walter 1973) for Jasper townsite, Alberta, 1061 m, 52° 53' N, 118° 04' W. Upper line is mean monthly precipitation; lower line is mean monthly temperature; solid bar is months with mean daily minimum temperature <0°C; hatched bar is months with extreme minimum temperatures <0°C; mean annual temperature is 2.9°C; mean annual precipitation is 401 mm; years of record is 44; mean frost-free period (1941-70) is 84 d. Temperatures on left, in descending order: extreme maximum, mean daily maximum warmest month, mean daily minimum coldest month, extreme minimum.

snowy winters, with cool and rainy summers (Dfb after Köppen). These conditions also exist in Banff and most other montane zones of the region. Jasper has a mean annual temperature of 2.9°C. The annual temperature range between the mean daily maximum of the warmest month and the mean daily minimum of the coldest month is 39.7°C, and the extreme range is 83.4°C. Diurnal fluctuations are high, compared with other regional stations. July, the warmest month, has a mean daily temperature of 15.1°C, and a mean daily maximum of 22.8°C. Summer temperatures exceed 21°C on one out of three days during June through August, and exceed 27°C on one out of five to six days during July and August. Frost can occur during any summer month but the frequency of occurrence is low (one day per month during June through August). The mean frost-free period (1941-1970 records) is 84 days (7 June-31 August) but extremes of 21 and 127 days have been recorded. January is the coldest month with mean daily temperatures of -11.8°C and mean daily minimum of -16.9°C. Winter minimum temperatures show greater deviations from the mean than summer. Cold temperatures are pronounced (especially in valleys) during winter. Extreme minimum temperatures of <-40 to -45°C have probably occurred in all areas of Jasper National Park. The probability (P) is >0.25 that temperatures <-30°C will be recorded during December and January and P>0.10 during November through February at Jasper townsite. Temperatures in the -25 to -30°C range occur during most years.

Higher elevations around Jasper townsite would show both a decrease in maximum and minimum temperatures and temperature range. The spring-fall lapse rates probably range between the moist (5.5°C/km) and dry (9°C/km) adiabatic lapse rates in the free atmosphere. Jasper National Park tends to be slightly more isothermal (i.e. lower lapse rate) than the other contiguous Parks (see Figs. 4.3b-d in Janz and Storr 1977). Free air mass stability is greater in winter than in spring and summer. Winter air temperatures are often isothermal up to ca. 2100 m. Temperatures at high elevations often vary little or are even warmer than valley sites. The frequency of very low temperatures is reduced at higher elevations. Inversions may be deep and prolonged in winter with cold air trapped in valleys. Summer inversions are less frequent and more diurnal in nature.

The precipitation regime of Jasper townsite is typically continental with extreme variations between years. The mean annual precipitation is 401 mm but extremes of 219 mm and 580 mm have been recorded. Precipitation occurs with a frequency of one day in three (yearly) with a maximum in June through August (13 days per month) and a minimum in February through May (7-9 days per month). Jasper is the least snowy of all reporting stations in the contiguous Parks (31.5% as snow) and the frequency of summer snow is low. Jasper has a high frequency (one year in six) of low autumn snowfalls, conditions that are usually associated with warm, dry, westerly flows, but occasionally with cold, dry periods. The maximum snowpack usually occurs in late March or April.

A more maritime precipitation regime is found at higher elevations. These areas experience less year to year variation, and more of the precipitation occurs during the winter, and as snow throughout the year. Rough estimates of precipitation on Signal Mountain may be derived from elevation versus precipitation equations of Janz and Storr (1977). The estimated mean annual precipitation for 2200 m would be about 600 mm with up to 80% occurring as snow. The maximum snowpack at higher elevations probably occurs in late April or May.

Microclimate

Limited microclimatic data are available for the alpine zone of Signal Mountain. La Roi (unpublished data) suggests that at timberline (ca. 2050 m) the mean annual temperature is ca. -4.5°C (annual lapse rate of 7.5°C/km from Jasper townsite) and annual precipitation may exceed 700 mm. Temperature (air, soil), radiation, precipitation, relative humidity, and wind data for July and August, 1967, are presented for Signal Mountain by Hrapko (1970) and Hrapko and La Roi (1978). Comparisons are made with Jasper townsite and between various microsites in the alpine zone. Diurnal temperature fluctuations were less on Signal than at Jasper. Maximum temperatures on Signal were consistently lower but minimums were often higher, particularly during warmer periods. Temperatures at +135 cm showed a maximum of 22°C and an absolute range of 38°C. Temperatures <0°C occurred on four dates. Greater diurnal variation occurred nearer the soil surface (+50 and +18 cm) but were reduced below ground (-2 and -10 cm). Frequent cloud cover, particularly in afternoons, reduced actual radiation from potential. Maximum and minimum daily irradiance values were 35.1 and 7.5 $MJ \bullet m^{-2} \bullet d^{-1}$, respectively. Precipitation during the study period was only 61% of Jasper's and approximately 18% occurred as snow. Relative humidity varied between 20 and 100% and the maximum vapor pressure deficit recorded was 2.2 kPa. Mean wind speeds at the fire lookout were 10.0 km/hr. Higher winds were usually associated with warmer weather or the warmest period of the day. Prevailing wind directions were WSW (from the Yellowhead Pass) but upslope S winds were also common and occasional NE winds occurred, usually associated with precipitation (particularly snow). Calm periods were rare and of short duration.

Microsite variability was high and slope aspect and other topographic features were more important than elevation in determining microclimates. Site variation was greater in maximum than in minimum temperatures. Temperatures (air and soil) and wind were positively correlated with exposure. South slope sites had higher maximum and minimum temperatures and wind speeds than north slope sites. Soil temperatures were negatively correlated with soil moisture and plant cover and were less at north slope sites.

The Study Years: 1973-1975

Inferences concerning the "normality" of the study years can be made by comparing Jasper townsite data for these years with the longterm record (see Fig. 9 for comparisons and Appendix for Atmospheric Enviroment Service data). This comparison can be used to project seasonal microenvironmental conditions for Cassiope habitats on Signal Mountain. It can be estimated that snow melt occurred early in 1973 due to above-normal winter temperatures and below-normal precipitation. The 1973 summer had near-normal temperatures, but was dry with high soil moisture deficits. Below-normal temperatures and above-normal precipitation in early winter 1973-74 resulted in early and deep snow cover. Snow release of Cassiope habitats was delayed in 1974. The 1974 summer had near-normal temperatures and the slight summer precipitation deficit was probably ameliorated by the late snow melt. Fall 1974 was dry with little snow. Snow cover was delayed and potential desiccating conditions existed through early winter. Plants in very exposed microsites might have been exposed to low temperature injury in mid winter. A near-normal year was probably represented in 1975, but with greatly fluctuating monthly temperatures and precipitation. Delayed melt of a below-normal snowpack probably resulted in near-normal snow release. The arrival of fall snow in 1975 was intermediate to 1973 and 1974.

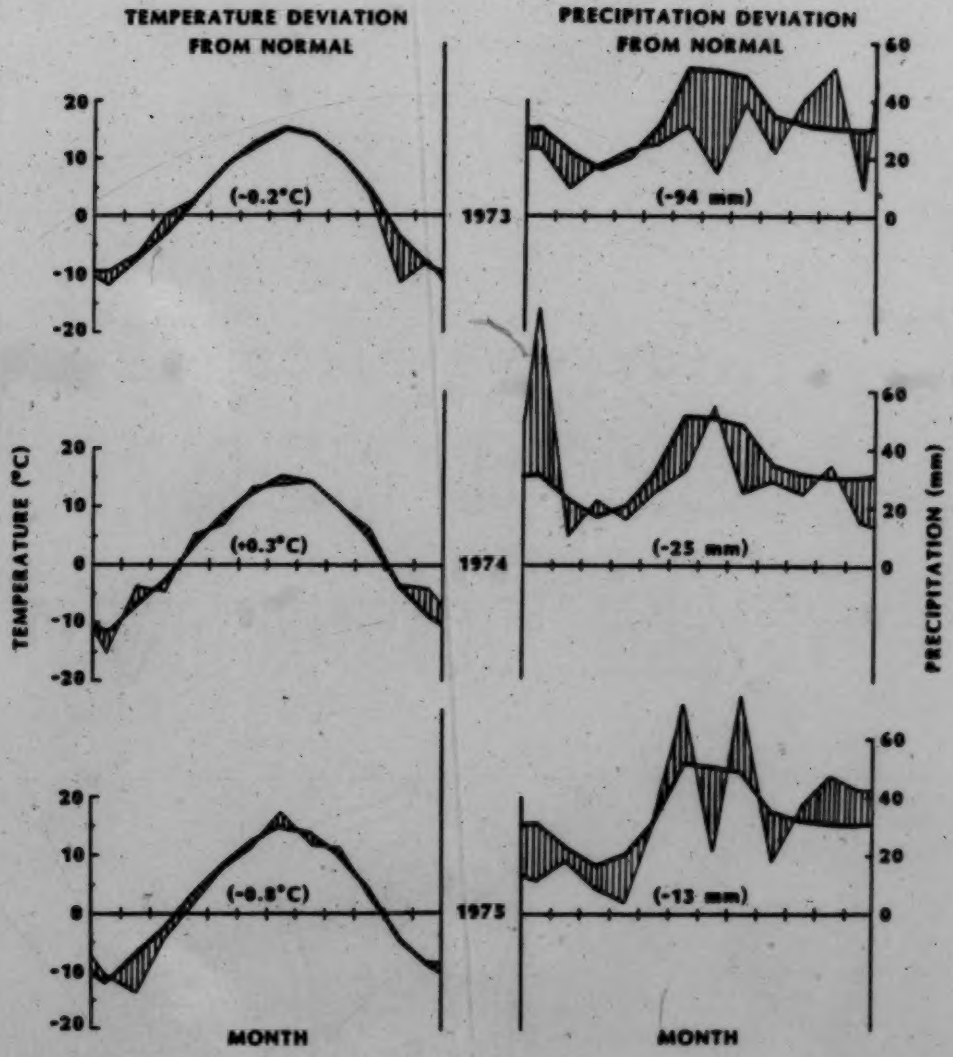


Figure 9. Monthly and (annual) deviation of temperature and precipitation (hatched) at Jasper townsite during the study years (1973-75) from 1926-75 'normals' (bold line).

The variability in the study years allows the following conditions to be accessed with respect to the proposed hypotheses concerning Cassiope habitat selection:

1. Documentation of the winter snow regime in years of above and below-normal winter precipitation and both early and late snow cover and release.
2. Documentation of the summer snow-free period in years of early and late snow release.
3. Possible soil moisture stess in a year (1973) of early snow release coupled with a summer precipitation deficit.
4. Possible desiccating conditions in fall and early winter (1974) due to above-normal temperatures and below-normal precipitation.
5. Possible periods of low temperature stress (late winter 1974-75) due to below-normal temperatures and precipitation.

III. THE CASSIOPE HABITAT

A. Vegetation and Environmental Gradients

1. Microtopography

a. Methods

A transect was established in 1973 at each Site to compare species distribution patterns, responses of *Cassiope* (growth rates, phenology, and water relations), and changes of environmental parameters along a topographic gradient. The transects extended downslope and crossed both the *C. tetragona* and *C. mertensiana* communities at each Site. The transects at Sites 1 and 2 were originally 52 and 60 m in length, respectively, but were extended in 1974 to 95 m to include a greater variety of habitats. They were marked with 2.75 and 4.25 m snow stakes (2.54 cm conduit) and were surveyed at 1 m intervals with a transit to establish a topographic profile.

b. Results

The mean slopes of Site 1 and 2 were 32.8 and 30.0%, respectively (Figs. 10 and 11). Small changes in microtopography of up to 1.3 m above or 0.3 m below the mean slope resulted in abrupt changes in community patterns and species distribution along the transect. Convex, upslope surfaces were more exposed and supported chionophobic species while concave, downslope surfaces were more protected and supported chionophilic species.

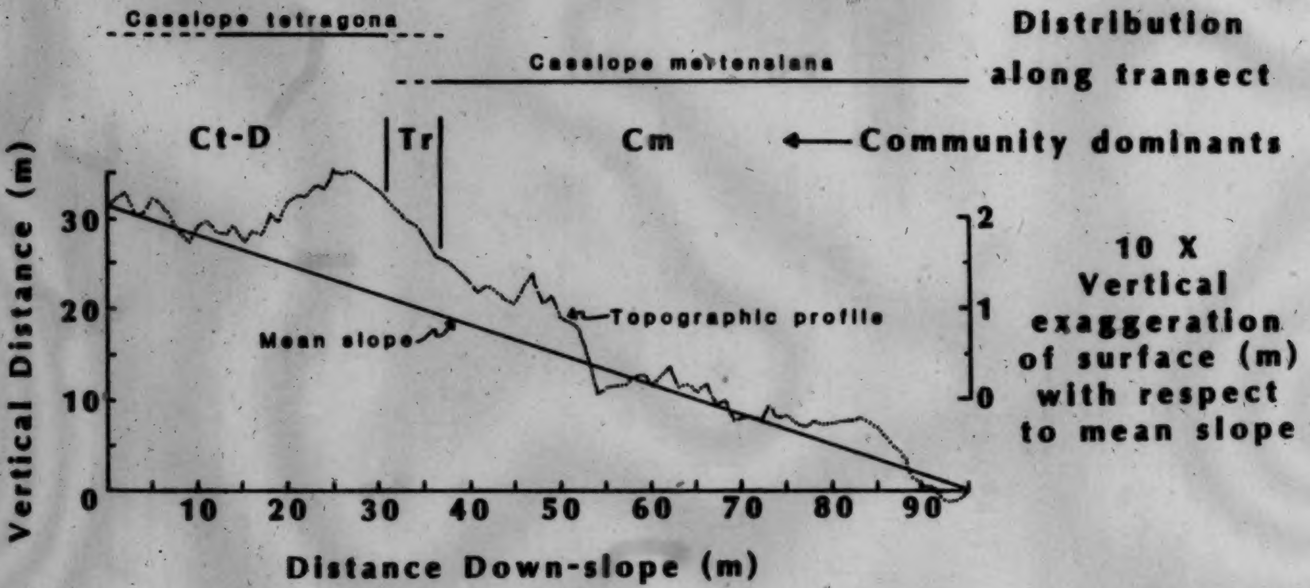


Figure 10. Topographic profile of Site 1 showing microtopography of surface, distribution of Cassiope spp. along the transect, and associated community dominants (Ct-D = Cassiope tetragona-Dryas; Tr = Transition; Cm = Cassiope mertensiana).

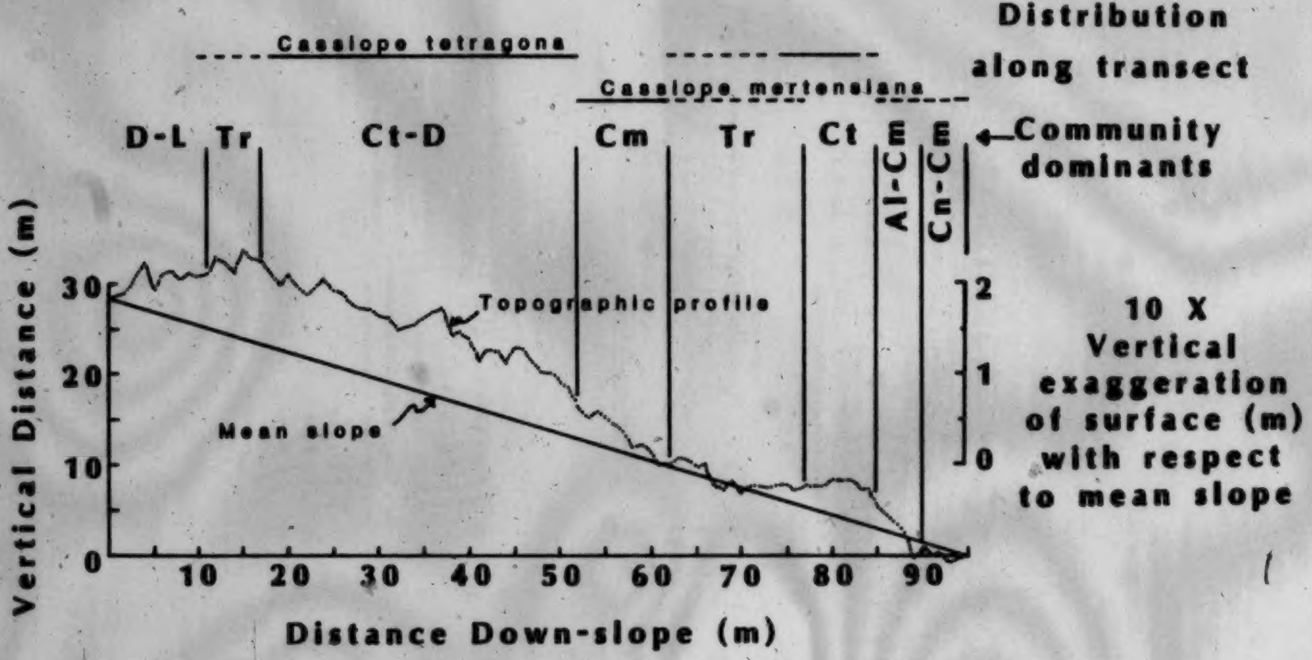


Figure 11. Topographic profile of Site 2 showing microtopography of surface, distribution of *Cassiope* spp. along the transect, and associated community dominants (D-L = *Dryas*-Lichen; Tr = Transition; Ct-D = *Cassiope tetragona*-*Dryas*; Cm = *Cassiope mertensiana*; Ct = *Cassiope tetragona*; Al-Cm = *Antennaria lanata*-*Cassiope mertensiana*; Cn-Cm = *Carex nigricans*-*Cassiope mertensiana*).

2. Vegetation

a. Methods

The vegetation along each transect was sampled in order to relate changes in species composition and structure to changing environmental parameters. Ten sample points were located at 4-15 m intervals along each transect, the spacing dependent upon the abruptness of observable vegetational or environmental gradients. At each sample point a 10 m line (bisected in the center) was laid out perpendicular to the transect, and ten 25 X 25 cm quadrats randomly placed along each line. Rectangular quadrats are commonly used but Eddleman *et al*. (1964) indicated that quadrat size and number are more important than quadrat shape for tundra vegetation. Size and shape were chosen to facilitate comparisons with other studies in the area (Hrapko 1970, Kuchar 1975, Hrapko and La Roi 1978, Mortimer 1978). A minimum of forty quadrats were placed in the primary plant community at each study Site. This was a 50 to 100% larger total sample size than used by the above researchers for similar vegetation and well beyond the point where the species-area curve began to flatten (Cain 1938).

Cover was estimated using a modified Braun-Blanquet--Daubenmire cover scale (Table 2). The median percentage cover of each class was used to calculate the average cover for a species. The narrow ranges of the lower cover classes are suitable for alpine vegetation in which many species have low cover. The broad ranges of the higher

Table 2. Cover scale used in vegetation sampling.

CLASS	PERCENTAGE COVER	MEDIAN
7	96-100%	98.0%
6	76- 95	86.0
5	51- 75	63.0
4	26- 50	38.0
3	16- 25	20.0
2	6- 15	10.0
1	1- 5	3.0
+	under 1	0.5
R	RARE	0.1

cover classes are less accurate and probably underestimate cover for these species.

Voucher specimens were collected from the two intensive Sites and have been deposited in the University of Alberta Herbarium. Nomenclature of vascular plants follows Moss (1959), except Minuartia (Wolf et al. 1979), and Dryas octopetala L.(instead of D. hookeriana Juz.). Nomenclature of bryophytes and lichens follow Crum et al. (1973), and Hale and Culberson (1970), respectively.

b. Results

Site 1

Cover of major vegetation components and dwarf shrubs along the transect at Site 1 are shown in Figs. 12 and 13 (see Table 3 for a complete listing of vascular species). The abrupt transition between communities and species that occurred at 35 m downslope was related to microtopography (see Fig. 10). Total vascular plant cover increased in the more protected areas downslope from a mean of 40% in the C. tetragona-Dryas community to 71% in the C. mertensiana community. Cassiope tetragona and Dryas octopetala were the major vascular species in the former community and together constituted 70% of the total vascular cover. Cassiope mertensiana constituted 70% of the total vascular cover downslope. Bryophyte cover was variable (4-16%) but slightly higher in the C. tetragona-Dryas community. Lichen cover was uniformly low (<5%). Litter was negatively correlated with total vascular cover due to the importance of Cassiope. Old leaves of Cassiope remain attached to the living shoots and decompose in situ, producing little litter. The amount of bare ground was negligible except at a locally disturbed area ca. 10 m.

Total number of vascular species sampled in the C. tetragona-Dryas community was 24, with a mean of 16 per sample point. The C. mertensiana community had greater diversity with 35 species sampled, and a mean of 21 per sample point. This was due to the presence of several alpine species in trace amounts and a larger number of subalpine species. Cassiope tetragona, Dryas octopetala, and Salix arctica had mean covers of 15, 13, and 3%, respectively, in the C. tetragona-Dryas community. Cassiope mertensiana and

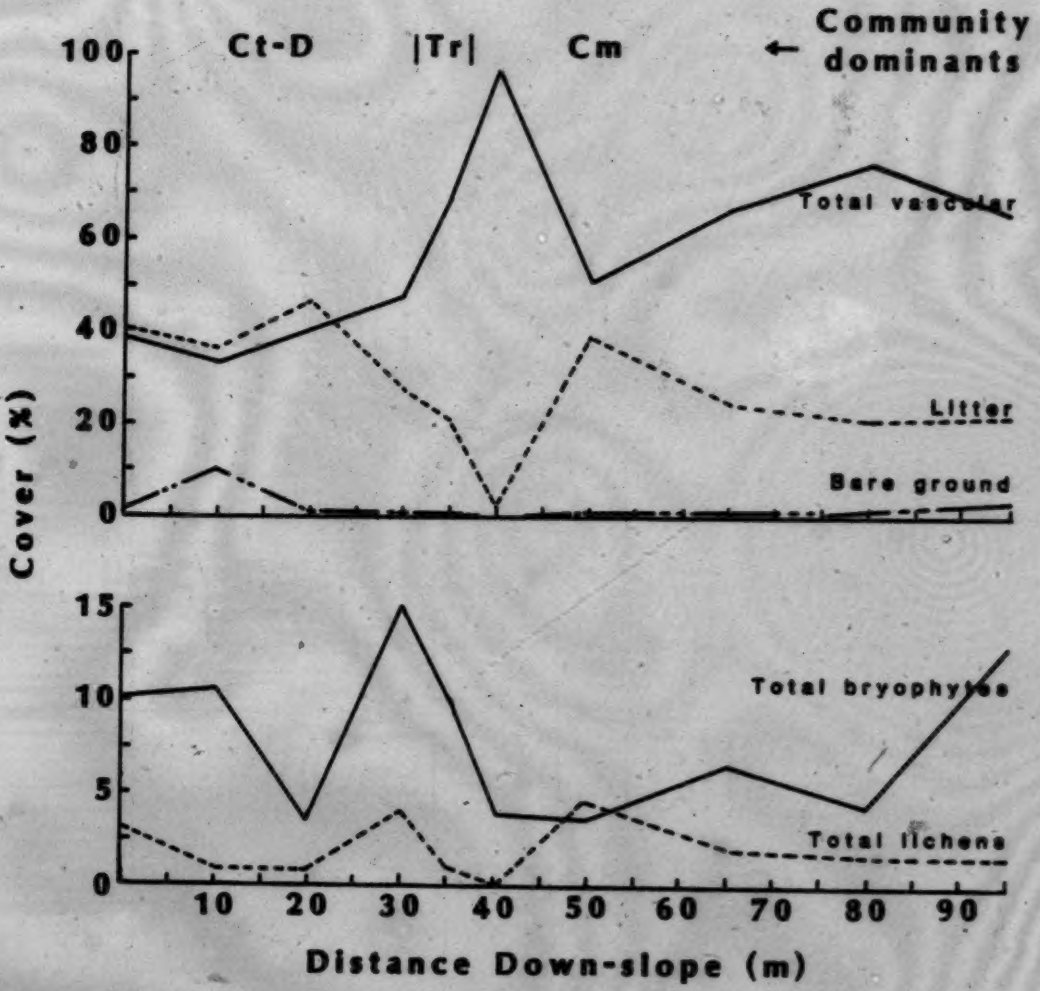


Figure 12. Cover of vegetation components along the transect at Site 1. See Fig. 10 for topographic profile and key to community dominants.

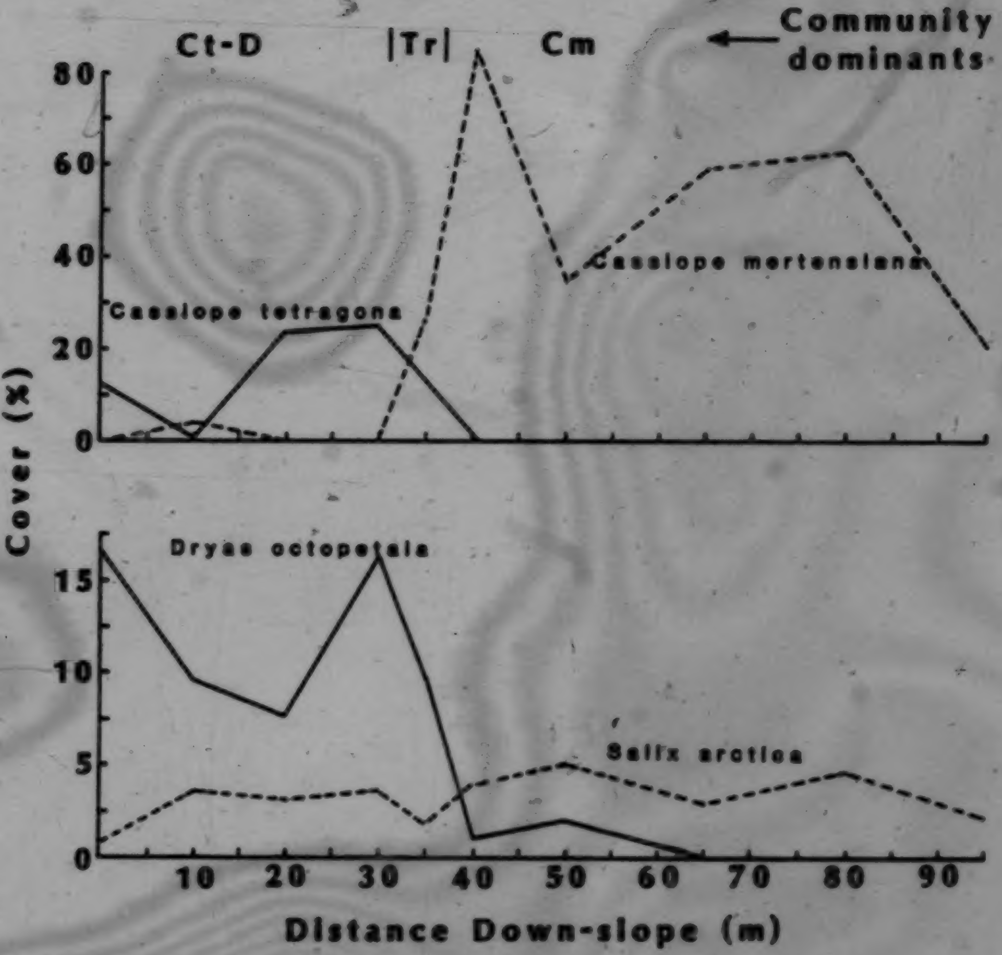


Figure 13. Cover of Cassiope spp. and major dwarf shrubs along the transect at Site 1. See Fig. 10 for topographic profile and key to community dominants.

Table 3. Percent cover of vegetation components and vascular species along the transect at Site 1. Species richness is indicated for each community or microsite. Cover values are means of 10 quadrats per sample point. Tr. = Cover <0.1%

	Cassiope tetragona - Dryas				Transition	Cassiope mertensiana				
	0m	10m	20m	30m	35m	40m	50m	65m	80m	95m
Vasculars	38.6	33.1	40.7	47.8	68.8	96.0	50.5	66.3	76.4	65.6
Bryophytes	10.8	12.3	3.7	15.6	10.6	4.0	3.7	6.6	4.3	12.5
Lichens	3.2	0.9	0.9	4.0	1.1	0.1	4.6	2.1	1.7	1.5
Litter	40.6	36.2	46.8	27.5	21.1	2.6	39.1	24.7	20.1	21.6
Bare Ground	1.6	10.0	1.3	0.7	1.3	0	0.8	0.9	1.3	3.8
Vascular Plants										
No. of Species										
Community	24					35				
Microsite	13	18	16	17	25	19	25	19	23	17
Cassiope tetragona	12.5	0.4	23.7	25.1	12.5	--	--	--	0.3	--
Dryas octopetala	16.6	8.6	7.6	16.2	9.7	1.0	2.0	--	--	--
Carex Spp.	1.0	1.0	tr.	0.3	--	--	--	--	--	--
Pedicularis capitata	0.5	1.2	0.4	0.3	0.4	tr.	tr.	--	--	--
Equisetum scirpoides	0.4	0.1	0.4	tr.	tr.	tr.	--	--	--	--
Potentilla diversifolia	0.4	0.3	0.4	0.4	--	--	tr.	--	--	--
Polygonum viviparum	0.2	0.4	0.2	0.2	0.1	--	0.1	--	--	--
Unidentified forbs	1.0	0.3	--	0.1	--	--	tr.	--	--	--
Solidago multiradiata	tr.	--	--	0.3	--	tr.	--	--	--	--
Phyllodoce glanduliflora/ intermedia	3.8	9.3	4.0	--	14.6	2.0	1.6	0.3	3.6	4.8
Salix arctica	0.7	3.5	3.2	3.6	1.8	3.9	5.0	2.9	4.6	1.5
Artemisia norvegica	1.4	0.2	0.5	0.7	0.4	2.0	1.0	1.4	0.3	0.3
Poa arctica	tr.	tr.	0.1	0.2	tr.	--	tr.	0.2	tr.	tr.
Arnica latifolia	--	0.2	0.2	0.4	0.5	1.6	0.1	0.7	0.4	0.1
Erigeron perigrinus	--	2.2	0.1	tr.	0.3	0.4	0.6	0.4	tr.	--
Campanula lasiocarpa	--	0.2	tr.	--	tr.	--	--	tr.	tr.	--
Antennaria lanata	--	tr.	--	--	0.3	tr.	0.3	0.1	1.4	1.0
Sibbaldia procumbens	--	0.2	--	--	tr.	--	0.1	0.1	tr.	tr.
Cassiope mertensiana	--	4.0	--	--	26.3	81.5	34.8	58.7	62.4	52.5
Ranunculus escholtzii	--	--	--	--	tr.	tr.	0.1	tr.	--	tr.
Carex Sp.A	--	--	tr.	--	--	--	--	--	--	--
Carex Sp.B	--	--	--	tr.	1.0	0.4	tr.	--	0.3	--
Carex Sp.C	--	--	--	tr.	--	0.6	0.9	0.6	tr.	0.7
Lycopodium selago	--	--	--	tr.	0.4	--	--	--	--	--
Veronica alpina	--	--	--	--	tr.	1.1	0.4	0.1	1.3	--

Table 3. (continued)

	Cassiope tetragona - Dryas				*Transition*	*Cassiope mertensiana*				
	0m	10m	20m	30m	35m	40m	50m	65m	80m	95m
Castilleja occidentalis	--	--	--	--	tr.	--	--	--	tr.	--
Hieracium gracile	--	--	--	--	tr.	--	--	tr.	0.6	0.1
Poa alpina	--	--	--	--	tr.	--	0.2	--	0.4	0.2
Festuca baffinensis	--	--	--	--	tr.	--	0.2	--	--	--
Luzula parviflora	--	--	--	--	tr.	0.3	0.8	0.3	tr.	0.7
Carex Sp.D	--	--	--	--	tr.	0.4	0.1	--	tr.	0.8
Senecio triangularis	--	--	--	--	--	0.4	--	--	--	tr.
Juncus drummondii	--	--	--	--	--	0.3	0.4	0.1	0.1	0.4
Silene acaulis	--	--	--	--	--	--	1.1	tr.	--	--
Trisetum spicutum	--	--	--	--	--	--	tr.	--	--	--
Poa cusickii	--	--	--	--	--	--	--	0.1	0.3	2.3
Carex nigricans	--	--	--	--	--	--	--	0.2	tr.	--
Petasites frigidus	--	--	--	--	--	--	--	--	0.6	--

Salix arctica had mean covers of 52 and 4% in the *C. mertensiana* community. The only other species with high cover was *Phyllodoce glanduliflora*/*intermedia*, but it was more important in the transition zone between the communities. All other species were of minor importance with cover values <1-2%.

Vascular species found in greater abundance in the *C. tetragona*-*Dryas* community include *Pedicularis capitata*, *Potentilla diversifolia*, *Polygonum viviparum*, and *Equisetum scirpoides*. Most of these are alpine constants in mesic habitats. The dominant bryophytes were *Hylocomium splendens*, *Dicranum acutifolium*, *Pohlia cruda*, and *Hypnum revolutum*. Lichens were predominantly fruticose species including *Cetraria islandica* and *Cladonia* spp. Vascular species found in greater abundance in the *C. mertensiana* community include *Veronica alpina*, *Antennaria lanata*, *Luzula parviflora*, and *Juncus drummondii*. The dominant bryophytes were *Brachythecium* sp., *Barbilophozia lycopodioides*, *B. hatcheri*, and *Pseudoleskeella tectorum*. Lichens were predominantly foliose species including *Peltigera canina* and *P. aphthosa*. Several species were common in both communities including the alpine species *Salix arctica*, *Artemisia norvegica*, and *Poa alpina*, the subalpine species *Phyllodoce glandulifora*/*intermedia*, *Arnica latifolia*, and *Erigeron perigrinus*, and the bryophyte, *Drepanocladus uncinatus*. The presence of these latter is indicative of the protected nature of this study Site. The *C. tetragona*-*Dryas* community at this site was more mesic and differed structurally and floristically from the C. tetragona-Dryas community at Site 2.

Site 2

Cover of major vegetation components and dwarf shrubs along the transect at Site 2 are shown in Figs. 14 and 15 (see Table 4 for a complete listing of vascular species). Community patterns and species distributions were more complicated than at Site 1 and microtopography (see Fig. 11) exerted a greater influence at this more exposed alpine Site. Total vascular plant cover was lowest in the Dryas-lichen community ($\bar{X}$ = 27%), intermediate in the C. tetragona-Dryas community ($\bar{X}$ = 49%), and highest in the C. mertensiana community ($\bar{X}$ = 76%). The latter two were comparable to their respective communities at Site 1. Dominance was even more highly restricted at Site 2, and in both the C. tetragona-Dryas and C. mertensiana communities, 82% of the total vascular cover was contributed by the indicator species. Cassiope mertensiana was only a minor component (% cover) of the Antennaria lanata/Carex nigricans-C. mertensiana communities but it provides a characteristic physiognomy to these areas dominated by small herb and graminoid species. Bryophyte cover was comparable to the respective communities at Site 1 and was again higher in the C. tetragona-Dryas community ($\bar{X}$ = 13%) than in the C. mertensiana community ($\bar{X}$ = 6%). Bryophyte cover was low in the exposed Dryas-lichen community ($\bar{X}$ = 5%) and the Carex nigricans- C. mertensiana community ($\bar{X}$ = 4%). Litter was

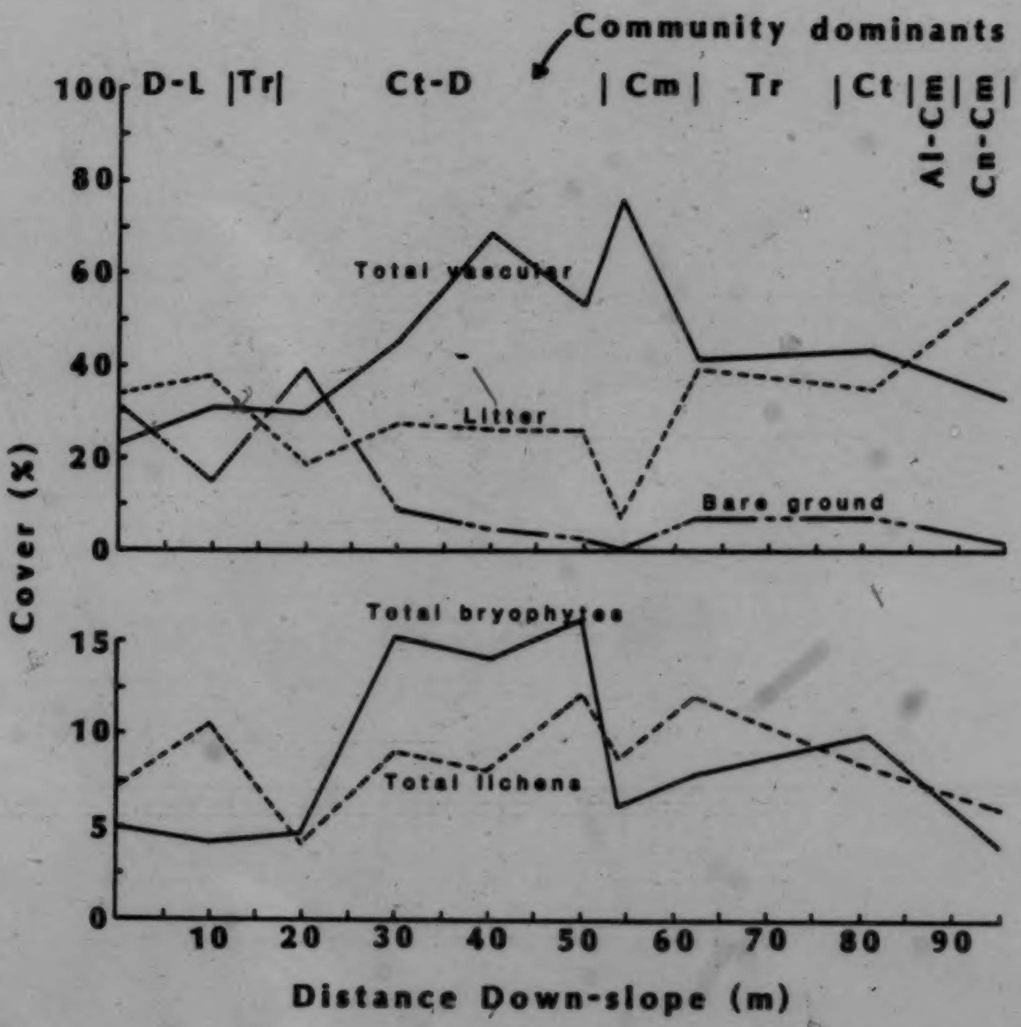


Figure 14. Cover of vegetation components along the transect at Site 2. See Fig. 11 for topographic profile and key to community dominants.

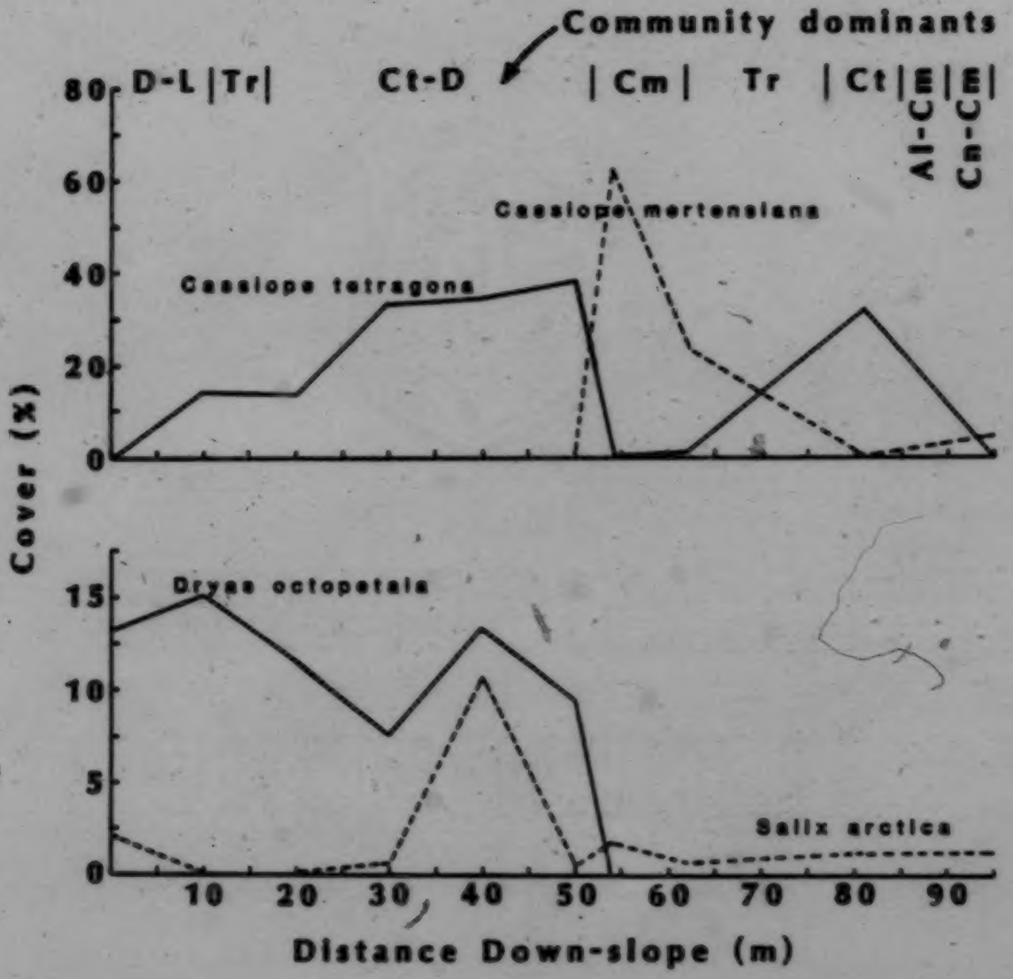


Figure 15. Cover of Cassiope spp. and major dwarf shrubs along the transect at Site 2. See Fig. 11 for topographic profile and key to community dominants.

Table 4. Percent cover of vegetation components and vascular species along the transect at Site 2. Species richness is indicated for each community or microsite. Values are means of 10 quadrats per sample point. Tr. = Cover <0.1%

	Dryas-lichen		Cassiope tetragona-Dryas				Cassiope mertensiana	Transition	Cassiope tetragona	Carex nigricans C. mertensiana
	0m	10m	20m	30m	40m	50m	54m	62m	81m	95m
Vasculars	23.0	31.1	29.8	44.8	68.9	52.5	76.0	41.2	43.8	33.0
Bryophytes	4.9	4.1	4.6	15.3	14.2	16.3	6.1	7.8	10.0	4.0
Lichens	6.5	10.6	4.1	9.1	8.1	12.2	8.8	12.1	8.3	6.1
Litter	33.9	37.9	18.7	27.8	26.1	16.0	7.2	39.4	35.6	58.3
Bare Ground	31.3	14.7	39.4	9.2	4.2	2.4	0.4	7.3	7.7	2.0
Vascular Plants										
No. of Species										
Community	23		28							
Microsite	20	14	18	15	16	16	13	16	17	17
Dryas octopetala	13.2	15.2	11.6	7.7	13.4	9.5	tr.	--	tr.	--
Cassiope tetragona	--	14.2	13.9	33.2	34.4	37.9	0.6	1.3	31.9	--
Salix arctica	2.0	tr.	0.3	2.7	12.4	2.0	6.8	2.9	4.6	4.6
Salix nivalis	0.5	0.1	tr.	0.2	1.4	2.1	0.9	1.0	0.3	0.3
Silene acaulis	1.3	tr.	1.0	--	0.3	tr.	0.1	--	--	--
Oxytropus podocarpa	3.0	tr.	--	--	--	--	--	--	--	--
Carex rupestris	0.4	0.2	--	--	--	tr.	--	--	--	--
Pedicularis capitata	0.1	--	tr.	tr.	0.6	tr.	--	--	tr.	--
Poa alpina	tr.	tr.	tr.	--	0.4	0.1	tr.	0.4	--	--
Campanula lasiocarpa	tr.	tr.	tr.	tr.	tr.	tr.	--	tr.	--	--
Polygonum viviparum	tr.	tr.	tr.	tr.	tr.	--	--	--	0.2	tr.
Equisetum scirpoides	0.4	--	--	--	--	--	--	--	--	--
Arnica alpina	0.1	--	--	--	--	--	--	--	--	--
Draba Sp.	tr.	--	--	--	--	--	--	--	--	--
Selaginella densa	tr.	0.6	--	--	--	--	--	--	--	--
Potentilla nivalis	tr.	--	tr.	--	--	--	--	--	--	--
Minuartia austromontana	tr.	--	tr.	--	--	--	--	tr.	0.1	tr.
Stellaria longipes	tr.	--	tr.	--	--	--	--	--	--	--
Carex spectabilis	tr.	tr.	--	tr.	0.3	--	--	--	--	--
Antennaria alpina	tr.	--	0.3	tr.	tr.	--	--	--	--	--
Festuca baffinensis	tr.	--	0.4	tr.	--	tr.	--	--	--	--
Vaccinium vitis-idaea	--	0.7	1.4	--	--	--	--	--	tr.	--
Unidentified Forb	--	tr.	--	--	--	--	--	--	--	--

Table 4. (continued)

	Dryas-lichen		Cassiope tetragona-Dryas				Cassiope mertensiana	Transition	Cassiope tetragona	Carex nigricans C. mertensiana
	0m	10m	20m	30m	40m	50m	54m	62m	81m	95m
Minuartia obtusiloba	--	--	0.3	--	--	--	--	--	--	--
Pyrola grandiflora	--	--	0.4	--	--	--	--	--	--	--
Luzula spicata	--	--	tr.	tr.	tr.	tr.	--	0.2	--	--
Hierochloe alpina	--	--	--	0.6	0.3	tr.	--	--	--	--
Gentiana glauca	--	--	--	tr.	--	tr.	--	--	--	--
Carex Sp. E	--	--	--	tr.	--	--	--	--	--	--
Abies lasiocarpa	--	--	--	0.3	--	--	--	--	--	--
Artemisia norvegica	--	--	--	--	4.8	0.5	0.4	5.2	1.8	2.0
Potentilla diversifolia	--	--	--	--	0.4	tr.	1.8	0.1	0.4	tr.
Carex Sp. F	--	--	--	--	0.1	0.1	0.5	--	--	--
Cassiope mertensiana	--	--	--	--	--	--	62.0	23.5	--	4.8
Antennaria lanata	--	--	--	--	--	--	2.6	1.7	0.5	4.8
Castelleja occidentalis	--	--	--	--	--	--	tr.	1.4	0.6	0.4
Poa arctica	--	--	--	--	--	--	tr.	--	--	--
Carex nigricans	--	--	--	--	--	--	--	0.2	0.8	6.8
Lycopodium alpinum	--	--	--	--	--	--	--	2.0	--	--
Sibbaldia procumbens	--	--	--	--	--	--	--	0.5	1.0	0.7
Ranunculus escholtzii	--	--	--	--	--	--	--	0.4	--	0.2
Trisetum spicatum	--	--	--	--	--	--	--	--	tr.	--
Luzula wahlenbergii	--	--	--	--	--	--	--	--	1.0	2.2
Carex Sp. G	--	--	--	--	--	--	--	--	0.4	--
Veronica alpina	--	--	--	--	--	--	--	--	--	0.8
Erigeron perigrinus	--	--	--	--	--	--	--	--	--	1.4
Poa cusickii	--	--	--	--	--	--	--	--	--	0.8
Juncus drummondii	--	--	--	--	--	--	--	--	--	3.0

lowest in the C. mertensiana community ($\bar{X}$ = 7%), intermediate in the C. tetragona-Dryas community ($\bar{X}$ = 25%), and highest at the two ends of the exposure gradient (Dryas-lichen $\bar{X}$ = 36%, Carex nigricans-C. mertensiana $\bar{X}$ = 58%). Percent bare ground followed a pattern directly related to exposure and was lowest in the C. mertensiana community and highest in the Dryas-lichen community.

Total numbers of vascular species sampled were highest in the C. tetragona-Dryas community (28) and Dryas-lichen community (23), and lowest in the C. mertensiana community (13). Mean number of species per sample point in the C. tetragona-Dryas community was similar to Site 1 but the C. mertensiana community was floristically depauperate. Mean cover of C. tetragona (30%) and C. mertensiana (62%) was higher than their respective communities at Site 1. Dryas octopetala had a mean cover of 14 and 11% in the Dryas-lichen and C. tetragona communities, respectively, the latter similar to Site 1. Salix arctica and S. nivalis were ubiquitous, the former with a mean cover of 4 and 7% in the C. tetragona-Dryas and C. mertensiana communities, respectively, and the latter in small amounts (generally <1%) in all areas.

The Dryas-lichen community had a large number of caespitose and mat forming species, all of low cover. The dominant bryophytes were Dicranum acutifolium, Pogonatum alpinum, and Rhytidium rugosum. Lichens were abundant including Cladonia spp., Cetraria spp., and crustose species. The *C. tetragona*-*Dryas* community had many vascular species of low cover (generally <1%), including *Pedicularis capitata*, *Campanula lasiocarpa*, *Polygonum viviparum*, *Antennaria alpina*, *Festuca baffinensis*, *Luzula spicata*, *Hierochloe alpina*, and *Artemisia norvegica*. Several of these were shared with Site 1. The dominant bryophytes were *Drepanocladus uncinatus*, *Dicranum acutifolium*, and *Hylocomium splendens*. Lichens were predominantly fruticose species including *Cladonia* spp., *Cladina mitis*, *Cetraria* spp., *Dactylina arctica*, and *Stereocaulon tomentosum*. *Antennaria lanata* and *Potentilla diversifolia* were the only forbs with cover >1% in the *C. mertensiana* community. The bryophytes and lichens were similar to Site 1. Subalpine vascular species and foliose lichens, including *Solorina crocea*, were more common in less exposed areas downslope.

3. Snow Cover

a. Methods

Snow depths were measured periodically at 1 m intervals along each transect to show patterns of fall-winter snow accumulation and spring-summer snow release. Measurements at Site 1 were taken on eight dates during the snow-covered periods of 1973-74 and 1974-75, and three dates during the summer and fall of 1975. Measurements at Site 2 were taken on seven and eight dates during 1973-74 and 1974-75, respectively, and three dates during the summer and fall of 1975. Total Site 1 transect coverage in 1973-74 was 50 m, including 11 m in the *C. tetragona*-*Dryas* community and 33 m in the *C. mertensiana* community. Transect extension in 1974 increased total coverage to 95 m, including 31 m in the *C. tetragona*-*Dryas* community and 58 m in the *C. mertensiana* community. Total Site 2 transect coverage in 1973-74 was 60 m, including 34 m in the *C. tetragona*-*Dryas* community and 8 m in the *C. mertensiana* community. Transect extension in 1974 increased total coverage to 95 m and coverage in the *C. mertensiana* community to 10 m, and added additional coverage downslope. This included 9 m coverage in a *C. tetragona* community (late snow release), and 5 m coverage in both an *Antennaria lanata*-*C. mertensiana* community and a *Carex nigricans*-*C. mertensiana* community. Mean and maximum community snow depths along the entire transect length are therefore not directly comparable between the years, but specific microsites and general patterns of accumulation and ablation can be compared.

b. Results

Site 1

Patterns of snow accumulation and ablation at Site 1 for 1973-74 and 1974-75 are shown in Figs. 16 and 17, respectively. Snowfall occurred in late September, 1973, and by 6 October, *C. mertensiana* was completely covered in all microsites although snow depths were not taken at this time. The tops of many of the large hummocks within the *C. mertensiana* community protruded above the snowpack but were vegetated by more chionophobic species including *C. tetragona*. Most other *C. tetragona* microsites were also

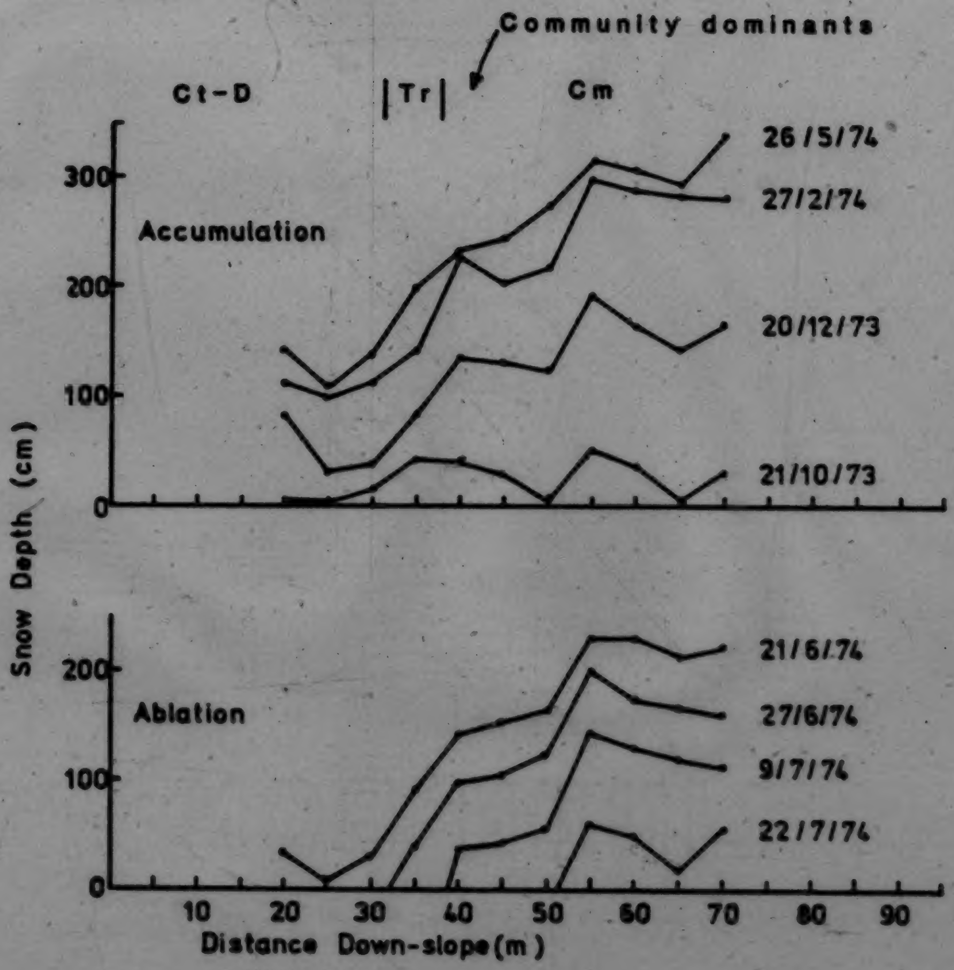


Figure 16. Patterns of snow accumulation and ablation along the transect at Site 1 during the winter of 1973-74. See Fig. 10 for topographic profile and key to community dominants.

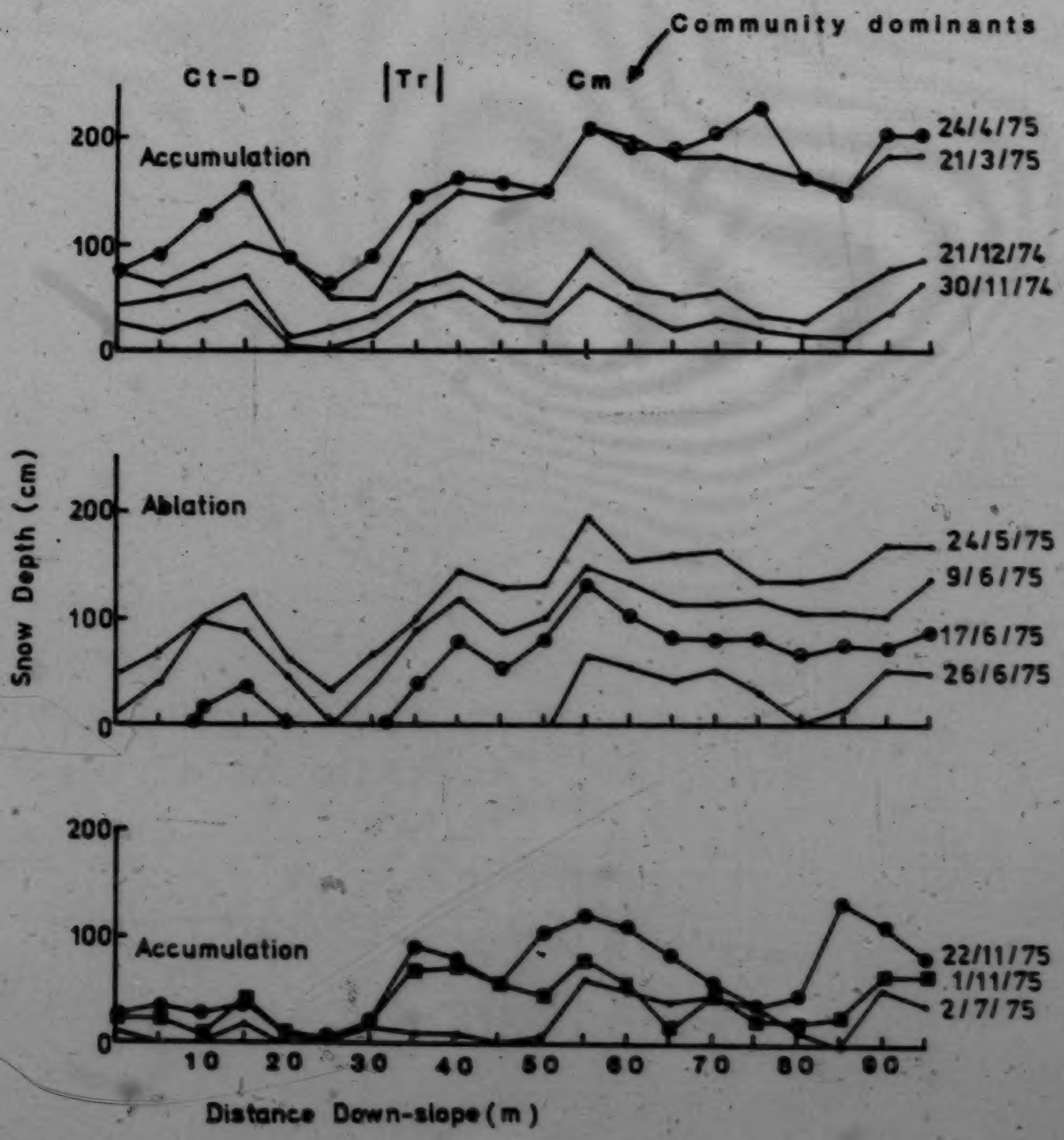


Figure 17. Patterns of snow accumulation and ablation along the transect at Site 1 during the winter of 1974-75, and summer-fall of 1975. See Fig. 10 for topographic profile and key to community dominants.

exposed. This same pattern was observed in all study years. The first appreciable late fall and early winter snowfalls were redistributed by wind into topographic depressions covering C. mertensiana which remained covered until spring. However, C. tetragona was rarely covered by these early snowfalls and often protruded above the snowpack in exposed microsites even in mid winter. Up to 50 cm of snow was present in the C. mertensiana community by 21 October, while <10 cm was present in the C. tetragona-Dryas community. Heavy snowfalls occurred during the winter of 1973-74 and maximum accumulations were recorded on 26 May, 1974. Snow depths at this time varied from 107 to 145 cm in the C. tetragona-Dryas community and from 222 to 340 cm in the C. mertensiana community. Snow release in 1974 was delayed by the deep snowpack. The C. tetragona-Dryas community began snow release on 22 June and was completely snow free by 3 July. The C. mertensiana community began snow release on 9 July but was not completely snow free until 2 August.

Snowfall was delayed in the fall, 1974, and accumulations in late November were comparable to those one month earlier in 1973. Maximum snow depths were measured on 24 April and varied from 56 to 158 cm in the C. tetragona-Dryas community and from 134 to 230 cm in the C. mertensiana community. Snow release of the C. tetragona-Dryas community began on 9 June and was complete by 19 June. Snow release of the C. mertensiana community began on 17 June but heavy snows (29.2 mm water equivalent) on 27-29 June delayed complete release until 10 July.

Early winter snow accumulations in 1975 were intermediate in depth and time of arrival to accumulations in 1973 and 1974. The C. mertensiana community was completely covered by late October, and by 22 November, 40 to 138 cm snow had accumulated. Many C. tetragona plants projected above the snowpack on this latter date and snow depths in the C. tetragona-Dryas community varied from 2 to 46 cm.

Site 2

Patterns of snow accumulation and ablation at Site 2 for 1973-74 and 1974-75 are shown in Figs. 18 and 19, respectively. Cassiope mertensiana was completely covered by snow in early October and by 21 October, 32 to 57 cm of snow was present in the C mertensiana community. Snow depths in the C. tetragona-Dryas community on this date varied from 2 to 35 cm with many plants projecting above the snowpack. Maximum snow depths were measured on 25 May, 1974, and varied from 60 to 164 cm in the C. tetragona-Dryas community and from 175 to 230 cm in the C. mertensiana community. The C. tetragona-Dryas community began snow release on 14 June and was completely snow free by 2 July. The C. mertensiana community began snow release on 5 July and was snow free by 16 July.

Winter and spring observations in 1973-74 indicated that vegetation patterns and species distributions were more highly influenced by microtopography and patterns of snow

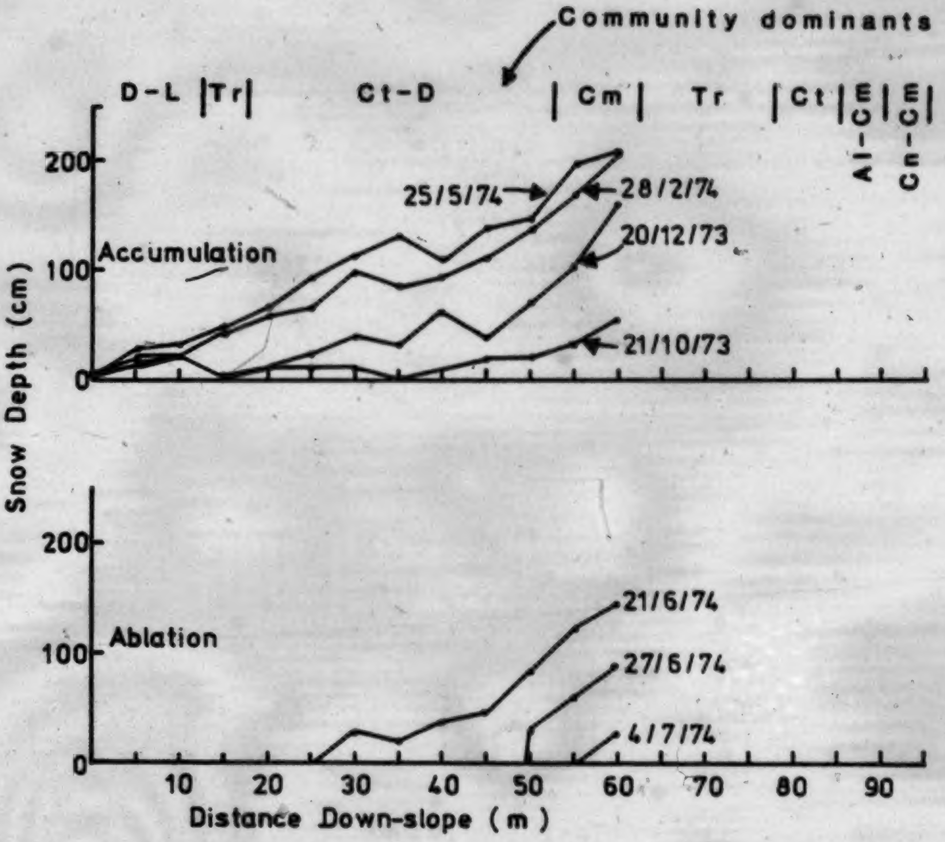


Figure 18. Patterns of snow accumulation and ablation along the transect at Site 2 during the winter of 1973-74. See Fig. 11 for topographic profile and key to community dominants.

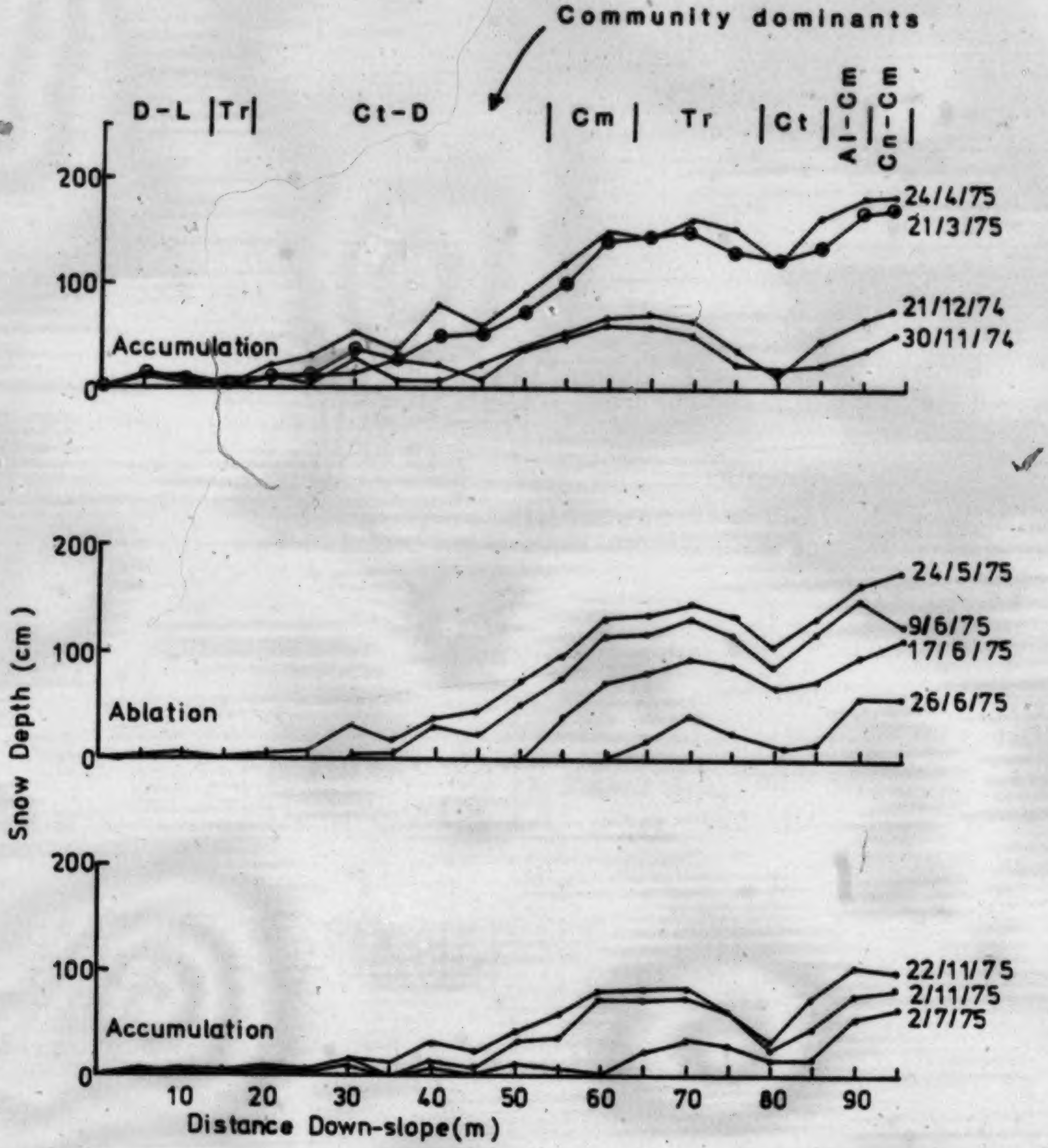


Figure 19. Patterns of snow accumulation and ablation along the transect at Site 2 during the winter of 1974-75, and summer-fall of 1975. See Fig. 11 for topographic profile and key to community dominants.

accumulation and ablation at this low alpine Site than at Site 1. Cassiope mertensiana occurred only in depressional or protected areas where snow accumulated early. Subsequent snowfalls and redistribution by wind extended snowbanks downslope covering areas that were exposed in early winter. Cassiope tetragona often occurred in these microsites. By late winter, deep snow covered these areas resulting in late snow release. Transect extensions in 1974 allowed this pattern of late accumulation and release to be documented.

Snowfalls were light in late fall 1974, and accumulations on 30 November were comparable to those one month earlier in 1973. Snow depths on this date in the C. tetragona-Dryas community varied from 1 to 34 cm with many plants projecting above the snowpack. Snow depths in the C. mertensiana community varied from 50 to 72 cm with all plants covered. The C. tetragona community near the base of the slope also had low snow cover (4 to 25 cm) and many plants exposed. The Antennaria lanata-C. mertensiana community and Carex nigricans-C. mertensiana community had 27 to 46 cm and 39 to 55 cm snow, respectively, and all plants were covered. Maximum snow depths were measured on 24 April, 1975, one month earlier than 1974. Snow depths at this time varied from 9 to 120 cm in the C. tetragona-Dryas community and from 119 to 154 cm in the C. mertensiana community. Deep snow occurred near the base of the transect with 124 to 163 cm in the C. tetragona community, 171 to 186 cm in the Antennaria lanata-C. mertensiana community, and

180 to 195 cm in the *Carex nigricans*-*C*. *mertensiana* community. Snow release in 1975 began approximately two weeks earlier than in 1974. The *C*. *tetragona*-*Dryas* community began snow release on 27 May and was snow free by 18 June. The *C*. *mertensiana* community began snow release on 22 June and was snow free by 4 July. Snowfall on 27-29 June delayed release of the *C*. *tetragona*, *Antennaria lanata*-*C*. *mertensiana*, and *Carex nigricans*-*C*. *mertensiana* communities. The release of all three communities occurred between 4 July and 6 July. In some areas of late and deep snow accumulation adjacent to this study Site, *C*. *tetragona* was not released until 10 July.

Early winter snow accumulations in 1975 were intermediate in depth and time of arrival to accumulations in 1973 and 1974. Snow depths on 22 November varied from 37 to 76 cm in the *C*. *mertensiana* community and from 2 to 51 cm in the *C*. *tetragona*-*Dryas* community. Snow depths were 33 to 75 cm in the *C*. *tetragona* community, 75 to 104 cm in the *Antennaria lanata*-*C*. *mertensiana* community, and 98 to 108 cm in the *Carex nigricans*-*C*. *mertensiana* community near the base of the transect.

c. The *Cassiope* Snow-Covered Period

The duration of continuous snow cover and snow release for the various *Cassiope* communities in the study years is shown in Fig. 20. The information from Figs. 16-20 is summarized in Table 5. The dates of snow arrival and release, maximum snow depths, etc., should be used for

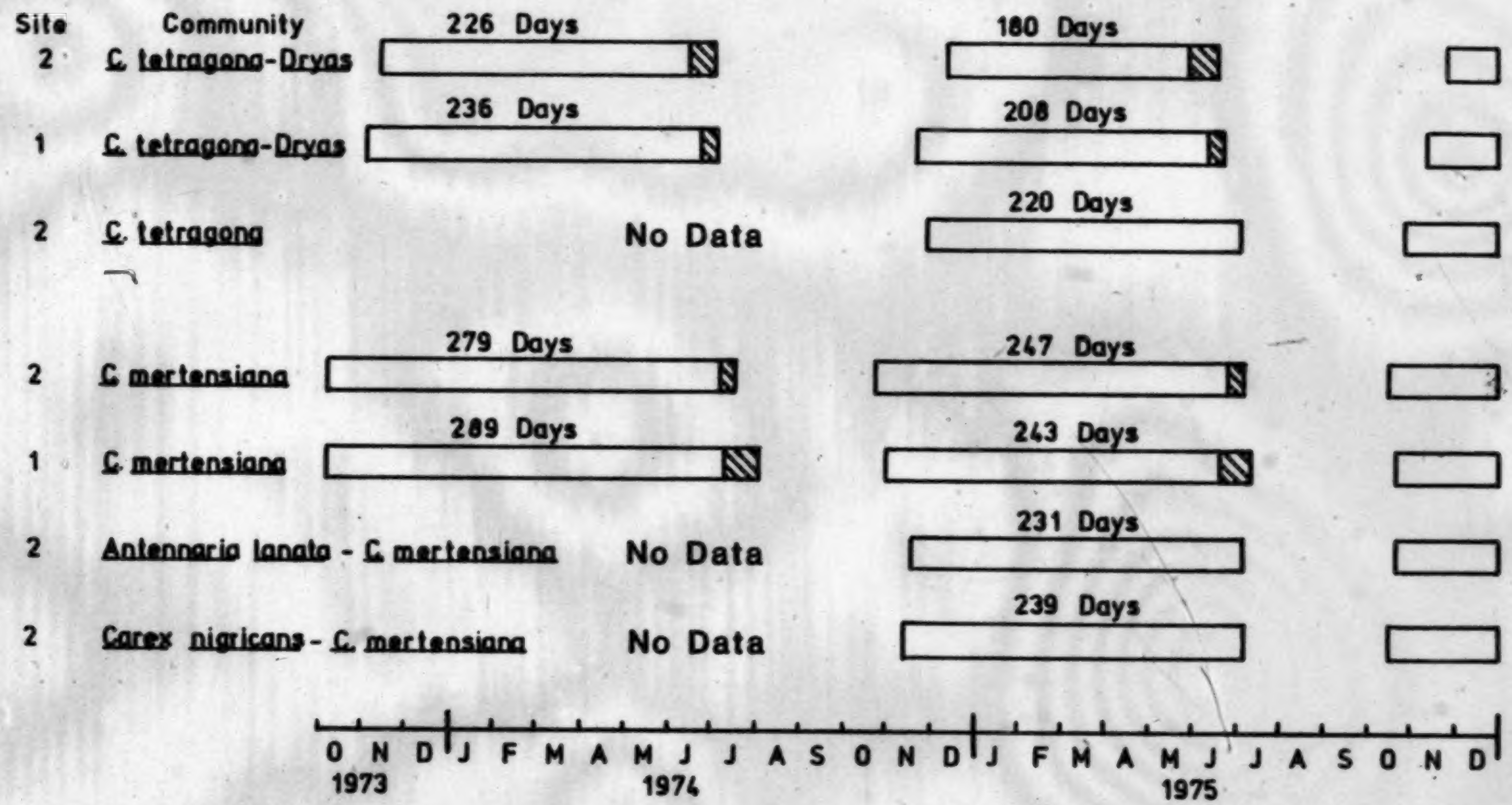


Figure 20. Duration of continuous snow cover (>15 cm) for C. tetragona and C. mertensiana communities at Sites 1 and 2. Initiation of snow cover is estimated date (± 7 days) that >50% of plants are covered. Cross hatching indicates snow release period. Days of snow cover are calculated to mid-points of snow release periods.

Table 5. Mean dates of arrival of continuous snow cover and snow release, length of snow-covered period, and maximum snow depths for *C. tetragona* and *C. mertensiana* communities at Sites 1 and 2.

SITE	COMMUNITY	$\bar{X}$ DATE ARRIVAL CONTINUOUS SNOW COVER a	DIFFERENCE FROM EARLIEST SNOW-COVERED COMMUNITY	$\bar{X}$ DATE SNOW RELEASE b	DIFFERENCE FROM EARLIEST SNOW-RELEASED COMMUNITY	$\bar{X}$ SNOW-COVERED PERIOD	$\bar{X}$ MAXIMUM SNOW DEPTHS c	%
2	*C. tetragona*-*Dryas*	25 Nov.	+41 Days	15 June	0 Days	203 Days	84 cm	100%
1	*C. tetragona*-*Dryas*	10 Nov.	+26	22 June	+7	225	114	136
2	*C. tetragona*	5 Nov. d	+21	12 July e	+27	250 f	179 e	213
2	*C. mertensiana*	15 Oct.	0	5 July	+20	264	171	204
1	*C. mertensiana*	19 Oct.	+4	10 July	+25	265	221	263
2	*Antennaria lanata*-*C. mertensiana*	28 Oct. d	+13	13 July e	+28	259 f	226 e	269
2	*Carex nigricans*-*C. mertensiana*	22 Oct. d	+7	14 July e	+29	266 f	240 e	286

a Estimated dates (± 7 days) that >50% plants covered by >15 cm snow. (1973, 1974, 1975 data)
b Mid-point snow-release period. (1974, 1975 data)
c Calculated from yearly $\bar{X}$ maximum snow depths. (1974, 1975 data)
d Normalized from 1974 and 1975 data.
e Normalized from 1975 data.
f Calculated from normalized dates.

microsite comparisons only and not be considered as absolute values. However, the data probably represents a close approximation of the "normal" conditon even though winter precipitation varied appreciably between the study years (see Microclimate Section). Greater than normal precipitation in October-November 1973, and January 1974, resulted in the early and deep snow cover and late release during these years. Similarly, unusually light precipitation during October-May 1974-75, resulted in the late, shallow snow cover and early release during these years. Jasper townsite precipitation for early winter (October-December) and late winter (January-May) for the period of study averaged 109 and 95%, respectively, of the 1926-75 mean. Total winter precipitation for the study period averaged 101% of the long term record.

Cassiope _mertensiana_ was usually snow covered by mid or late October. Snow arrived first and persisted at higher elevations where air and soil temperatures were cooler, but redistribution by wind soon covered the lower elevation areas. The dates in Table 5 for the arrival of continuous snow cover in the _Antennaria_ _lanata_-_C_. _mertensiana_ and _Carex_ _nigricans_-_C_. _mertensiana_ communities are somewhat anomalous. These community types usually experience snow cover as early or earlier than adjacent _C_. _mertensiana_ communities. The lateness of snow cover in these particular microsites is due primarily to the entrapment of snow by the _C_. _mertensiana_ community directly upslope (see Fig. 11). As previously stated, with the first appreciable late fall or early winter snowfall, all *C. mertensiana* plants were covered in all low alpine and upper subalpine habitats. Snow usually did not persist in the *C. tetragona* habitats until 3-6 wk after adjacent *C. mertensiana* areas were covered, and many *C. tetragona* plants could be found projecting above the snowpack in exposed microsites even in mid winter. This pattern of complete versus partial snow cover presented a marked contrast. Maximum snow accumulations occurred in late winter, and were greater at the lower elevation, more protected sites. Snow depths in *C. mertensiana* habitats were >200% those in adjacent *C. tetragona* habitats. Snow release of *C. tetragona* usually occurred in mid June and approximately 3 wk later for adjacent *C. mertensiana*. Snow release occurred a few days earlier at higher elevations because of more shallow snow cover. The snow-covered period was >200 days for *C. tetragona* and 6-9 wk longer for *C. mertensiana*.

While both *Cassiope* species are generally considered as chionophilic, the winter environment separates them along gradients of snow cover and length of the snow-covered period. An almost absolute separation occurs with respect to time of arrival of continuous snow cover. *Cassiope mertensiana* is always completely covered by early snow while *C. tetragona* is never completely covered at this time. *Cassiope tetragona* is tolerant of deep and long lasting snow cover (e.g., *C. tetragona* community at Site 2), but such microsites are exposed in early winter. The hypothesis that C. tetragona is unable to withstand the shortened growing periods of late meltout sites is not substantiated. The hypotheses that C. mertensiana may be unable to tolerate either low air temperatures during fall and winter or desiccation in exposed microsites are given support.

4. Summer Soil Moisture

a. Methods

Soil moisture was measured periodically during the late summers of 1973 and 1974 with porous cup thermocouple psychrometers (Wescor, Logan, Utah). The sensors were placed at -5 cm beneath each species in a variety of microsites and were read within one hour of solar noon with a Wescor psychrometric microvoltmeter. The psychrometer readings were found to be extremely erratic and few were meaningful when related to changes in precipitation, radiation and temperature. This type of soil psychrometer was found to be totally inadequate for this study and is probably of only limited application in any soils which are cold, subjected to frequent freeze-thaw cycles, and have high heat fluxes. Even then, the manufacturer's calibration should not be trusted and the psychrometers should be recalibrated over the range of water potentials and temperatures likley to be encountered.

Gravimetric soil moisture samples were collected along each transect at 1-2 wk intervals during the summer of 1975. Five microsites were sampled at Site 1 and eight microsites at Site 2. All samples were collected within a circle with a 1 m radius at each microsite. Samples of fine material (small stones and cobbles removed) were collected in duplicate from 0-5, 5-15, and >15 cm depths, and moisture content determined gravimetriclly (drying at 85-95°C for 24-48 h). Soil matric potential and water content at -0.03 and -1.50 MPa (0.33 and 15 bars pressure) were determined on composite samples from each microsite and depth using a ceramic pressure membrane apparatus (Soil Moisture Equipment Co., Santa Barbara, California).

b. Results

Seasonal soil moisture data are summarized in Tables 6 and 7. No soil moisture stress occurred during the summer of 1975 due to the frequency and amounts of precipitation. Mean seasonal soil moisture contents at all microsites and depths were greater than field capacity (-0.03 MPa) and no values were recorded below -1.50 MPa. No statistical differences were found in either the moisture holding capacity of the soils in different microsites or the mean seasonal soil moisture contents at specific depths in different microsites. However, both decreased with increasing soil depth. This may indicate some soil water depletion, but probably is more a function of decreasing organic matter contents and per cent of fines (<2 mm fraction) with depth. Only a slight trend was evident at the >15 cm depth at each Site relating minimum seasonal soil moisture contents or per cent of samples less than field capacity to the relative

Table 6. Summary of mean seasonal soil moisture along transect at Site 1 during summer, 1975. Values are g H_2O / g dry weight soil, percent of field capacity, or percent of samples less than field capacity.

	COMMUNITY & DISTANCE ALONG TRANSECT				
	C. tetragona-Dryas		C. mertensiana		
	3 m	26 m	38 m	60 m	85 m
0-5 cm Depth					
H_2O content at -0.03 MPa	0.50	0.58	0.48	0.36	0.37
H_2O content at -1.50 MPa	0.18	0.21	0.29	0.12	0.10
$\bar{X}$ Seasonal H_2O content & % of -0.03 MPa value	0.97 195%	1.33 230%	1.30 271%	0.79 221%	0.67 181%
Minimum seasonal H_2O content	0.56	0.99	0.67	0.45	0.46
% of samples <-0.03 MPa	0%	0%	0%	0%	0%
5-15 cm Depth					
H_2O content at -0.03 MPa	0.45	0.41	0.37	0.41	0.49
H_2O content at -1.50 MPa	0.14	0.08	0.12	0.08	0.10
$\bar{X}$ Seasonal H_2O content & % of -0.03 MPa value	0.68 151%	0.68 167%	0.59 160%	0.61 151%	0.69 142%
Minimum seasonal H_2O content	0.53	0.21	0.35	0.39	0.40
% of samples <-0.03 MPa	0%	17%	10%	11%	11%

Table 6. (continued)

	COMMUNITY & DISTANCE ALONG TRANSECT				
	C. tetragona-Dryas		*C. mertensiana*		
	3 m	26 m	38 m	60 m	85 m
>15 cm Depth					
H_2O content at -0.03 MPa	0.40	0.29	0.47	0.33	0.39
H_2O content at -1.50 MPa	0.13	0.07	0.11	0.07	0.09
$\bar{X}$ Seasonal H_2O content & % of -0.03 MPa value	0.55 136%	0.38 133%	0.59 124%	0.47 142%	0.64 162%
Minimum seasonal H_2O content	0.31	0.19	0.46	0.28	0.41
% of samples <-0.03 MPa	25%	50%	11%	13%	0%

NO VALUES WERE RECORDED BELOW -1.50 MPa AT ANY MICROSITE OR DEPTH.

Table 7. Summary of mean seasonal soil moisture along transect at Site 2 during summer, 1975. Values are g H_2O / g dry weight soil, percent of field capacity value, or percent of samples less than field capacity.

	COMMUNITY & DISTANCE ALONG TRANSECT							
	Dryas-lichen	*C. tetragona*-*Dryas*			*C. mertensiana*	Transition	*C. tetragona*	*A. lanata*/ *C. nigricans*- *C. mertensiana*
	1 m	19 m	37 m	50 m	56 m	70 m	80 m	90 m
0-5 cm Depth								
H_2O content at -0.03 MPa	0.37	0.45	0.39	0.53	0.38	0.34	0.39	0.37
H_2O content at -1.50 MPa	0.14	0.19	0.13	0.12	0.09	0.07	0.09	0.09
$\bar{X}$ Seasonal H_2O content & % of -0.03 MPa value	1.14 309%	1.15 253%	0.81 208%	1.00 191%	0.72 190%	0.74 220%	0.61 159%	0.75 203%
Minimum seasonal H_2O content	0.24	0.81	0.44	0.77	0.36	0.45	0.55	0.60
% of samples <-0.03 MPa	25%	0%	0%	0%	10%	0%	0%	0%
5-15 cm Depth								
H_2O content at -0.03 MPa	0.28	0.54	0.45	0.55	0.44	0.45	0.46	0.40
H_2O content at -1.50 MPa	0.08	0.11	0.10	0.12	0.08	0.09	0.08	0.08
$\bar{X}$ Seasonal H_2O content & % of -0.03 MPa value	0.54 190%	0.83 153%	0.51 113%	0.86 157%	0.56 129%	0.65 145%	0.62 135%	0.61 151%
Minimum seasonal H_2O content	0.19	0.22	0.35	0.71	0.36	0.52	0.50	0.48
% of samples <-0.03 MPa	25%	25%	36%	0%	22%	0%	0%	0%

Table 7. (continued)

	COMMUNITY & DISTANCE ALONG TRANSECT							
	Dryas-lichen	*C. tetragona*-*Dryas*			*C. mertensiana*	Transition	*C. tetragona*	*A. lanata*/ *C. nigricans*- *C. mertensiana*
	1 m	19 m	37 m	50 m	56 m	70 m	80 m	90 m
>15 cm Depth								
H_2O content at -0.03 MPa	0.24	0.34	0.36	0.48	0.34	0.38	0.42	0.36
H_2O content at -1.50 MPa	0.07	0.09	0.09	0.10	0.07	0.07	0.07	0.07
$\bar{X}$ Seasonal H_2O content & % of -0.03 MPa value	0.28 120%	0.52 153%	0.50 138%	0.75 156%	0.48 141%	0.52 138%	0.47 113%	0.49 136%
Minimum seasonal H_2O content	0.18	0.17	0.31	0.64	0.24	0.32	0.32	0.32
% of samples <-0.03 MPa	40%	18%	9%	0%	22%	13%	38%	13%

NO VALUES WERE RECORDED BELOW -1.50 MPa AT ANY MICROSITE OR DEPTH.

exposure of the microsites.

The seasonal progression of soil moisture at 5-15 cm depth is shown in Figs. 21 and 22. Similar trends occurred at the other sample depths, varying only in the actual amount of water present or the magnitude of change. Soil moisture contents were generally highest immediately after thaw. Periods of reduced soil moisture occurred in mid July and August. The first coincided with a period of 13 consecutive days without measurable precipitation that followed a heavy snowfall in late June. Snow accumulations in protected microsites persisted for up to seven days, delaying snow release of some Site 2 communities and causing a lag in the period of reduced soil moisture with respect to the more exposed microsites. The August depression coincided with a period of five consecutive hot, dry days and was not as distinct at the Site 2 protected microsites as at other Site 1 and Site 2 microsites. Soil moisture content leveled off above field capacity in late August and September.

Summer precipitation in 1975 at Jasper townsite was 102% of the 1926-75 record so the summer soil moisture data probably represents a near "normal" condition. Less precipitation occurred during the summers of 1973 and 1974 (58 and 76% of the long term record, respectively), and apparently drier soils were observed. However, unwise reliance on soil psychrometers precluded any meaningful soil moisture data during those years. The frequency of measurable precipitation is high during the summer in the

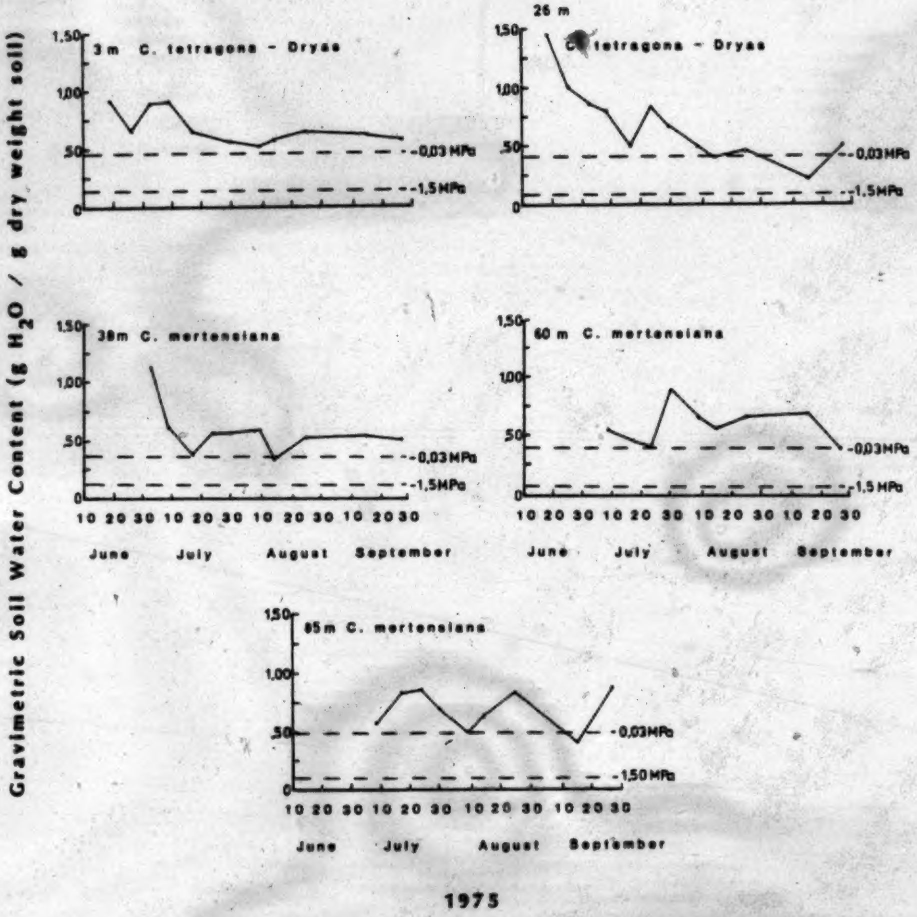


Figure 21. Seasonal soil moisture at 5-15 cm in several microsites along the transect at Site 1 during summer, 1975. Community dominants, distance down-slope (m), and -0.03 and -1.50 MPa moisture equivalents are indicated.

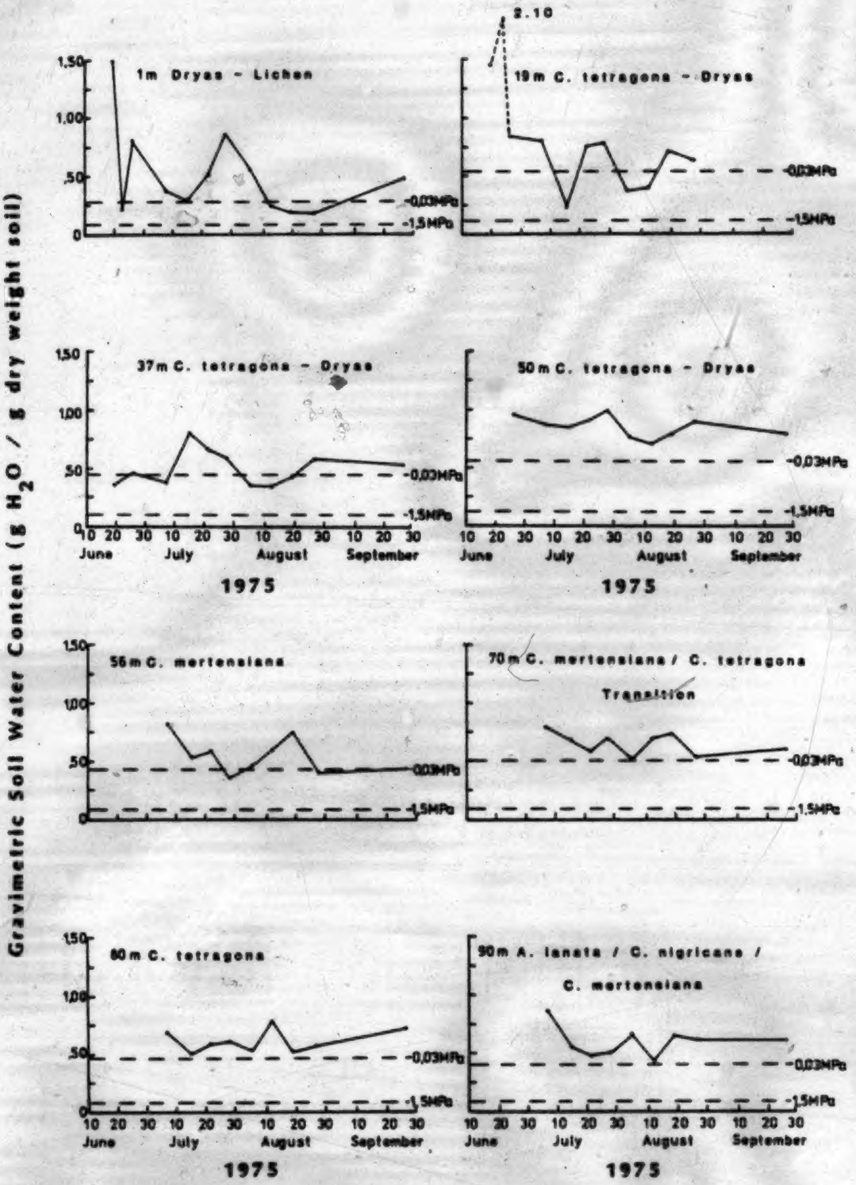


Figure 22. Seasonal soil moisture at 5-15 cm in several microsites along the transect at Site 2 during summer, 1975. Community dominants, distance down-slope (m), and -0.03 and -1.50 MPa moisture equivalents are indicated.

Jasper area. The longest recorded period without measurable precipitation during the summer months of 1973-75 was 17 days in September, 1975, too late in the season to affect plant growth or result in soil moisture stress. July averaged the greatest number of consecutive days without measurable precipitation ($\overline{X} = 10$ for 1973-75 period), followed by June and September ($\overline{X} = 8$), and August ($\overline{X} = 5$). Dry periods during June and September are probably ineffectual in causing soil moisture stress as the former comes before or during snow release of many microsites and the latter are coupled with lower temperatures and a cessation of plant growth. Twelve consecutive days without measurable precipitation were recorded during mid summer (July and August) in both 1974 and 1975, but only in 1974 was the period actually dry and not influenced by cloudy weather or delayed snow melt.

Although the 1975 data showed no differences in soil moisture in the various microsites, the protected C. mertensiana microsites most certainly experience a more favorable summer soil moisture regime in most years than the exposed C. tetragona microsites. Cassiope mertensiana microsites would have more soil moisture available at depth due to the delayed snow release and thawing of deeper horizons. Large rocks often form a basal core to the frost hummocks and inhibit thawing and downward water movement as evidenced by occasional gleying in the C horizon. This was rarely observed in the C. tetragona microsites, except in those areas of greater snow accumulation (e.g. *C. tetragona* community at Site 2). Utilization of this deeper source of soil moisture would extend the favorable growing period into mid summer in the *C. mertensiana* microsites, even in years of shallow snowpack coupled with an early snow release and a hot, dry summer.

Cassiope mertensiana is also probably more capable than *C. tetragona* of utilizing the frequent, light precipitation that often occurs in late summer and fails to penetrate deep into the soil. Both species produce extensive roots and rhizomes that penetrate to the C horizon at about 15 cm depth. Both species also produce adventitious roots, but they are more abundant in *C. mertensiana*, arising from most decumbent shoots and thoroughly permeating the LFH and surface soil horizons. The more dense plant canopy of *C. mertensiana*, and reduced wind speeds in the protected microsites and within the plant canopy, probably result in a greater catch of this light precipitation and an increased resistance to its loss to the atmosphere.

B. Soils

a. Methods

Soil pits were excavated in the *C. mertensiana* and *C. tetragona*-*Dryas* communities at Sites 1 and 2 and in three additional areas encompassing the range of habitats occupied by the two species in the upper subalpine and alpine zones on Signal Mountain. Extensive Site 3 was located at 2010 m on a 25% N slope, just within the *Picea*-*Abies* closed forest with a dense understory of *C*. *mertensiana* and *Vaccinium scoparium* on hummocky microtopography. Extensive Site 4 was located at a prominent snow depression at 2135 m on a 24% N slope (see Fig. 7). Peripheral microsites supported *C*. *tetragona*-*Dryas* while *C*. *mertensiana* occurred in the center on large frost hummocks (to 0.5 m height). Extensive Site 5 was a very exposed location on the summit ridge at 2225 m on a 5% N slope. *Cassiope tetragona* occurred only as scattered clumps in protected microsites. Soils were described and classified according to the System of Soil Classification for Canada (Canada Soil Survey Committee 1978).

Composite samples were collected from each described horizon and the <2 mm fraction subjected to physical and chemical laboratory analyses. Soil color (moist and dry) was described using Munsell color charts in natural daylight. Particle size analysis was done by the hydrometer method. Analytical methods for organic matter, pH, conductivity, and nutrients were those used by the Alberta Soil and Feed Testing Laboratory. Organic carbon was measured by Walkley-Black wet oxidation and converted to percent organic matter by multiplying by 1.72; pH was of a 1:2 soil to water paste; conductivity was corrected back to a saturated paste; N (NO_3^{-1}) was determined by the phenoldisulfonic method; P ($P_2O_5^{-2}$) was determined colorimetrically using a modified Bray and Kurtz extracting solution with combined nitric acid, vanadate, and molybdate; K was determined by flame photometry on an ammonium acetate extract; and cation exchange capacity (CEC) and exchangeable bases (Ca, Mg, Na, and K) were determined by flame photometry and atomic absorption spectrophotometry on an ammonium acetate extract.

b.Results

The soils of Cassiope habitats have been tentatively classified as Orthic Dystric and Eutric Brunisols. Soils of these same areas were described by Hrapko and La Roi (1978) as Orthic Sombric Brunisols which reflects the diversity and heterogeneity of these poorly developed alpine soils. Soil descriptions for Sites 1 and 2 are typical and presented in Table 8 (see Appendix for Sites 3-5). These soils had thin, fibrous, densely rooted turfs (0-3 cm thick) which showed little decomposition and thus the L designation. This was underlain by a dark colored Ah horizon (3-12 cm thick) with high organic matter content (18-27%). The Brunisolic Bm horizon (6-22 cm thick) showed the characteristic shift to higher chromas and redder hues than the underlying horizons, and the lower boundary at 15-23 cm marked the usual penetration depth of Cassiope roots. No eluviated (Ae) horizons were observed. Soils at Site 4 were similar except the C. mertensiana microsite had more complex Bm horizons due to intense cryoturbation. The Site 3 soil lacked the Ah horizon reflecting differences in pedogenesis at this forested site. The soil at Site 5 beneath C. tetragona-Dryas differed little from other C. tetragona habitats even though adjacent unvegetated areas showed little soil development

Table 8. Soil profile descriptions at Sites 1 and 2.

Site 1 is located at 2060 m on a 32% N slope. Site 2 is located at 2195 m on a 30% N slope. The rapidly to moderately well drained pedons support communities of C. tetragona-Dryas and C. mertensiana in different microsites. Glacial till has been deposited on Precambrian siltstones and slate and mixed by colluvial action. Some aeolian deposits may be present. Nonsorted stepped frost boils are common in C. tetragona microsites and frost hummocks in C. mertensiana microsites. Gravel, cobbles, and stones are few in Ah horizons and increase with depth (>50% in C horizons). Some mixing of Ah and Bm horizons in C. tetragona and C. mertensiana microsites.

Horizon	Depth (cm)	Description
Site 1. (C. tetragona-Dryas): Orthic Dystric Brunisol		
L	1-0	Fibrous turf; abundant, fine to medium random roots; abrupt, irregular boundary; 0-2 cm thick.
Ah	0-6	Black (10 YR 2/1 m, 3/2 d) sandy loam; very weak, fine subangular blocky; loose, very friable; plentiful, very fine to coarse horizontal and oblique roots; clear, wavy boundary; 5-9 cm thick; strongly acid.
Bmy	6-16	Very dark grayish brown (10 YR 3/2 m, 4/3 d) sandy loam; very weak, fine subangular blocky; loose, very friable; medium oblique roots; some gravel and cobbles; clear, wavy boundary; 8-11 cm thick; strongly acid.
C	16 +	Olive brown (2.5 Y 4/4 m, 6/4 d) sandy loam; amorphous; very friable; plentiful gravel and cobbles; strongly acid.
Site 1. (C. mertensiana): Orthic Dystric Brunisol		
L	2-0	Fibrous turf; abundant, fine to medium random roots; wavy boundary; 1-3 cm thick.

Table 8. (continued)

Horizon	Depth (cm)	Description
Ah	0-5	Black (10 YR 2/1 m, 3/2 d) sandy loam; very weak, fine subangular blocky; loose, very friable; plentiful, very fine to coarse horizontal and oblique roots; clear, wavy boundary; 3-6 cm thick; very strongly acid.
Bmy	5-15	Very dark grayish brown (10 YR 3/2 m, 5/3 d) sandy loam; very weak, fine subangular blocky; loose, very friable; few, very fine to medium oblique roots; some gravel, cobbles, and stones at lower boundary; clear, irregular boundary; 7-12 cm thick; very strongly acid.
C	15 +	Light olive brown (2.5 Y 5/4 m, 6/4 d) sandy loam; amorphous; very friable; plentiful, gravel, cobbles, and stones; strongly acid.
Site 2. (*C. tetragona*-*Dryas*): Orthic Dystric Brunisol		
L	2-0	Fibrous turf; abundant, fine to medium roots and few, coarse roots; abrupt, wavy boundary; 0-3 cm thick.
Ah	0-6	Very dark gray (10 YR 3/1 m, 4/2 d) loamy sand; very weak, fine subangular blocky; loose, very friable; plentiful, very fine random roots and few, fine to medium random roots; clear to gradual, irregular boundary; 4-12 cm thick; very strongly acid.
Bmy	6-22	Dark brown (10 YR 3/3 m, 4/4 d) sandy loam; very weak, fine subangular blocky; loose, very friable; few, very fine to fine horizontal and oblique roots; gradual, irregular boundary; 6-22 cm thick; strongly acid.
C	22 +	Dark grayish brown (2.5 Y 4/2 m, 6/4 d) sandy loam; amorphous; loose, friable; abundant, flat and angular gravel; medium acid.

Table 8. (continued)

Horizon	Depth (cm)	Description
Site 2. (C. mertensiana): Orthic Eutric Brunisol		
L	1-0	Fibrous turf; abundant, fine to medium random roots; abrupt, wavy boundary; 0-2 cm thick.
Ah	0-7	Very dark gray (10 YR 3/1 m, 4/2 d) sandy loam; very weak, fine subangular blocky; loose, very friable; plentiful, very fine to medium roots; clear, wavy boundary; 5-10 cm thick; extremely acid.
Bmy	7-23	Brown (10 YR 4/3 m, 5/3 d) sandy loam; very weak, fine subangular blocky; loose, very friable; few, very fine to fine horizontal roots; plentiful, gravel, cobbles, and stones; clear, smooth to wavy boundary; 14-19 cm thick; medium acid.
C	23 +	Olive brown (2.5 Y 4/4 m, 6/4 d) sandy loam; amorphous; very friable; abundant, gravel, cobbles, and stones; slightly acid.

and were classified as Orthic Regosols.

All soils were high in sand content but maxima were found in Ah and C horizons and slightly lower levels in Bm horizons (Table 9). Sandy loam textural classes predominated. Silt content was inversely proportional to sand, and clay content was generally low (<10%). There was little marked variation in particle size distribution through the profiles except at Sites 4 and 5 where higher clay contents (up to 29%) were found in Bm horizons. This may suggest a lithological discontinuity in the sola. Silty clay loam textures were found at these Sites. Sand contents were higher, silt contents lower, and clay contents similar to those reported by Hrapko and La Roi (1978). Structure was poorly developed (very weak, fine subangular blocky to amorphous) at all Sites and horizons, and soil consistence was loose to friable reflecting the high sand content. Gravel (<7.5 cm), cobbles (7.5-25 cm), and stones (>25 cm) were common in all soils; few were usually present in Ah horizons but they increased with depth and often constituted >50% (by volume) of Bm and C horizons.

Soils were acidic and pH values varied from 4.5 to 5.3 in Ah horizons (5.9 in Orthic Regosol at Site 5) and generally increased slightly with depth. Conductivities of all soils and horizons were low. Nutrient concentrations were also low; highest levels were found in Ah horizons and lower levels in Bm and C horizons. Nitrate-N varied from 4 ppm at the surface to trace amounts in the Bm and C

TABLE 9. PHYSICAL AND CHEMICAL PROPERTIES OF SIGNAL MOUNTAIN SUBALPINE AND ALPINE SOILS FROM *CASSIOPE* SPP. HABITATS.

SITE	SOIL SUBGROUP	HORIZON	DEPTH (cm)	% < 2 mm SAND	% < 2 mm SILT	% < 2 mm CLAY	TEXT. CLASS	pH (H_2O)	O.M. %	CONDUCTIVITY mmhos.	N (NO^-_3) ppm	P ($P_2O^-_5$) ppm	K (K+) ppm	Ca Meq./100g	Mg	Na	K	CEC	BASE SATURATION %
SITE 1: 2062m N ASPECT 32% SLOPE																			
C. tetragona — *Dryas*	0.DYB	L	1-0																
		Ah	0-6	71	24	5	SL	5.1	27.2	0.2	2	6	64	17.0	2.7	0.1	0.3	40.6	50
		Bmy	6-16	62	31	7	SL	5.1	17.4	0.1	1	1	37	6.0	0.9	0.1	0.2	26.9	27
		C	16+	78	11	11	SL	5.2	2.4	0.1	<1	1	50	2.7	0.7	TR	0.1	8.4	42
C. mertensiana	0.DYB	L	2-0																
		Ah	0-5	79	16	5	SL	4.6	26.2	0.3	1	5	86	11.3	1.9	0.1	0.4	37.2	37
		Bmy	5-15	69	24	6	SL	5.0	17.0	0.1	<1	1	26	4.9	0.7	0.1	0.1	26.9	22
		C	15+	78	12	9	SL	5.2	3.1	0.1	<1	<1	25	3.7	0.6	TR	0.1	10.2	43
SITE 2: 2193m N ASPECT 30% SLOPE																			
C. tetragona — *Dryas*	0.DYB	L	2-0																
		Ah	0-6	79	16	5	LS	4.6	18.1	0.2	4	6	67	7.1	1.2	0.1	0.2	20.9	31
		Bmy	6-22	71	10	9	SL	5.2	14.4	0.1	2	<1	31	5.0	0.7	0.1	0.1	29.3	20
		C	22+	77	12	11	SL	5.6	1.9	0.1	<1	1	70	5.1	1.6	TR	0.2	10.3	67
C. mertensiana	0.EB	L	1-0																
		Ah	0-7	81	14	6	SL	4.5	19.3	0.3	4	7	67	8.8	1.6	0.1	0.2	29.3	37
		Bmy	7-23	69	27	10	SL	5.8	9.5	0.1	1	0	23	5.3	0.9	0.1	0.1	18.1	35
		C	23+	71	20	9	SL	6.2	1.7	0.1	<1	1	24	5.8	2.0	TR	0.1	8.3	95
SITE 3: 2012m N ASPECT 25% SLOPE																			
Picea-Abies/ *C. mertensiana* *Vaccinium*	0.DYB	L	0-0																
		Bmy	0-22	67	24	9	SL	5.3	7.1	0.2	<1	1	31	7.7	0.9	0.1	0.1	20.2	45
		C	22+	75	11	14	SL	5.2	1.4	0.1	<1	<1	33	3.6	0.7	TR	0.1	7.5	59
SITE 4: 2130m N ASPECT 24% SLOPE																			
C. tetragona — *Dryas*	0.DYB	L	2-0																
		Ah	0-3	77	5	18	SL	5.1	19.6	0.3	<1	10	75	15.3	3.0	0.1	0.3	30.5	61
		Bmy	3-12	67	9	24	SCL	5.3	13.7	0.1	1	<1	37	5.8	1.1	0.5	0.2	31.8	24
		C	12+	78	10	12	SL	5.4	3.1	0.1	<1	1	43	3.5	1.2	TR	0.1	12.5	38
C. mertensiana	0.DYB	L	3-0																
		Ah	0-7	83	6	11	LS	4.2	20.5	0.2	<1	3	30	3.5	0.9	0.1	0.1	40.6	11
		Bmy1	7-13	70	8	22	SCL	4.9	6.9	0.1	<1	<1	24	1.4	0.4	0.1	0.1	18.1	11
		Bmy2	13-17	69	6	25	SCL	5.0	10.9	0.1	<1	<1	20	2.1	0.3	0.5	0.1	28.0	11
		Cgj	17+	59	13	29	SCL	4.9	3.2	0.1	<1	1	18	1.4	0.5	TR	0.1	13.1	15
SITE 5: 2225m N ASPECT 5% SLOPE																			
C. tetragona — *Dryas*	0.DYB	LFH	6-0																
		Ah	0-6	87	7	6	LS	4.7	19.3	0.3	<1	16	114	12.1	1.8	TR	0.4	36.0	40
		Bm1	6-12	69	9	22	SCL	5.0	12.9	0.1	2	<1	35	2.5	0.4	0.1	0.1	22.2	14
		Bm2	12-13	64	8	28	SCL	5.5	11.6	0.1	2	0	23	1.9	0.4	0.1	0.1	26.9	9
		C	13+	77	11	12	SL	5.5	1.7	0.1	<1	<1	28	2.5	1.5	TR	0.1	9.3	44
STONE PAVEMENT	0.R	Ah	0-3	92	7	1	S	5.9	6.5	0.2	1	8	94	7.6	1.5	TR	0.2	13.1	71
		C	3-20	86	8	6	LS	5.3	1.7	0.1	<1	1	51	2.6	1.1	0	0.1	6.4	58

A. 0.DYB = ORTHIC DYSTRIC BRUNISOL; 0.EB = ORTHIC EUTRIC BRUNISOL; 0.R = ORTHIC REGOSOL

B. TR = TRACE < 0.05

horizons. Phosphorus followed the same trend but with up to 16 ppm in the Ah horizon at Site 5. Potassium was found in higher concentrations (up to 114 ppm in Ah horizons) but levels were generally lower than those reported by Hrapko and La Roi (1978). Cation exchange capacities and exchangeable bases (Ca, Mg, Na, K) were low in all soils and horizons and decreased with depth. Calcium was the dominant exchangeable cation, Mg was in low concentrations, and Na and K only occurred in trace amounts.

Humus and clay contents, and pH influence greatly the concentration and availability of absorbed nutrients. Higher CEC's would be expected in horizons with higher humus or clay contents (thus the maxima in Ah horizons) but low concentrations of exchangeable bases would be found at lower pH values because of the low percentage base saturation; most colloidal sites would be occupied by tightly bound hydrogen and aluminum hydroxy ions. Availability of other nutrients (e.g. N and P) not bound to colloidal complexes is also reduced at lower pH values and soil temperatures. As a result, these soils are low in both the concentration and availability of nutrients. Both species of Cassiope have mycorrhizae which may aid in nutrient and water uptake. Also, the growth form and xeromorphic characteristics of Cassiope may be related to nutrient conservation in such sites.

C. Microclimates

a. Methods

The two intensive study Sites were instrumented to detect microclimatic differences. Air temperature and moisture, global radiation, wind, precipitation, and soil temperature and moisture were monitored using either recording instruments or by taking spot readings.

Continuous records were made of air temperature and relative humidity with hygrothermographs (Belfort Instrument Co., Baltimore, Maryland) housed in louvered aluminum shelters (after Vogel and Johnson 1965) placed on the ground surface. Sensor height was approximately 6-20 cm. Seven-day clocks were used during summer and 31-day clocks during winter. Shelters were situated in the center of the primary community at each Site during the 1973 summer (60 m and 30 m along transects at Sites 1 and 2, respectively). Due to late meltout they were moved to more exposed locations for 1974 and 1975 (25 m and 15 m along transects at Site 1 and 2, respectively). Winter snow accumulation necessitated placement of the Site 1 shelter on a platform at 2 m from December, 1974 to June, 1975. Shelters were lined with two thicknesses of percale sheeting (47 threads per cm) in winter to avoid accumulation and compaction of blowing snow. This probably caused a damping and lag in the recording of temperature and relative humidity. Instrument malfunctions occurred frequently during winter cold spells (_ca_. 50% of data lost). Vapor pressure deficit (VPD) was calculated from temperature (T °C) and relative humidity (RH) using the following equation (D.W.A. Whitfield pers. comm.):

$$\text{kPa VPD} = (0.61+T(4.44\times10^{-2}+T(1.43\times10^{-3}+T(2.62\times10^{-5}+T(2.96\times10^{-7}+2.56\times10^{-9}T)))))(1.0-RH/100) \quad (1)$$

Global radiation at Site 2 was recorded with a Belfort pyranometer placed on top of the shelter. The instrument was leveled and sensor height was approximately 70 cm. Records were made only during the summer months.

Summer precipitation was monitored daily with unshielded Tru-Check rain gauges (orifice leveled at 60 cm) placed at the 1973 shelter locations. These wedge-shaped gauges may be subject to considerable error during periods of wind or light rain because of turbulence at the corners of the orifice and water droplet adherance to the sides. Ethylene glycol and mineral oil were used to prevent freezing and evaporation. Winter snowfall was not measured but snow depths were periodically taken at 1 m intervals along a transect at each Site to show patterns of winter snow accumulation and spring snow release (see Vegetation and Environmental Gradients Section).

Wind speed was monitored at each Site with a Belfort 3-cup totalizing anemometer (cups leveled at 60 cm). The anemometers were situated in similar topographic positions as the instrument shelters, and as with the latter were moved to more exposed positions in 1974 to facilitate summer and winter measurements. Additional anemometers were installed during portions of the 1974 summer to provide direct comparisons between the _C_. _mertensiana_ and _C_. _tetragona_ communities at each Site.

Thermocouples (0.8 mm) were installed adjacent to the snow transect poles for measurement of air, snow, and soil temperatures during summer and winter months. Three series of thermocouples were installed at both communities at each Site. Sensor heights were 60, 10, 0, -5, -15, and -25 cm during the period October 1973 through October 1974, but were repositioned to 50, 10, 0, -10, -25, and -50 cm for the period October 1974 through 1975. Thermocouples were read with a psychometric microvoltmeter (Wescor. Logan, Utah); summer readings were taken within one hour of solar noon but winter readings were more variable. Additional thermocouples were installed at 0, -5, and -15 cm in various microsites and read periodically during the summers of 1973 and 1974.

Profiles of temperature, VPD and wind speed were taken above _Cassiope_ clumps during the summer of 1973. Readings were taken at hourly intervals from 0700 to 1900 h MST on three different days at Site 1 and two different days at Site 2. During each day's observations, readings were alternated on consecutive hours between microsites. Wind speeds were measured at 100, 50, 15, and 5 cm height with a thermopile anemometer with a uni-directional probe (Hastings-Raydist Inc., Hampton, Virginia). The latter two heights are at the top and within the plant canopy, respectively. Readings were taken at 15 s intervals alternating between the heights and with five replicates of the profiles. Instrument readings were corrected for elevation using the following equation supplied by Hastings-Raydist Corporation:

Corrected wind speed = Measured wind speed X P^{o}/P^{z}....(2)

where P^{z} is the atmospheric pressure at altitude z and P^{o} is atmospheric pressure at sea level (instrument calibration point). At 2128 m (mean elevation of study Sites): P^{o}/P^{z} = 101.3 kPa/78.3 kPa = 1.29.

Wet and dry bulb temperatures were measured concurrently at the same height with a Bendix aspirated psychrometer. VPD was calculated from RH using equation 1.

b. Results

The microclimate of the low alpine Site 2 is described. Environmental data are given in Figs. 23, 24 and 25 for 1973, 1974, and 1975, respectively, and are summarized in Table 10. The microclimate of Site 2 is representative of extensive areas on the northerly lee slope of Signal Mountain and probably similar sites in the Jasper region. The data are also more comparable with screen height (1.5 m) data from other studies due to the windy nature of the microsite, and are less influenced by the proximity of krummholz than Site 1. Comparisons are made between years, intensive Sites and microsites, and with Jasper townsite where applicable.

Global Radiation

Mean daily irradiance was highest in July, and varied from 18.5-21.3 $MJ \bullet m^{-2} \bullet d^{-1}$ during the three years. This is the month immediately following snow melt and corresponds with the period of greatest plant growth. The maximum daily value recorded was 30.1 $MJ \bullet m^{-2} \bullet d^{-1}$ in August, 1974, but daily values >25 $MJ \bullet m^{-2} \bullet d^{-1}$ were recorded in July and August of all three years. Radiation levels declined noticeably through August to *ca*. 13 $MJ \bullet m^{-2} \bullet d^{-1}$ in September. Variability was noted from year to year; 1973 and 1974 were seasonally comparable, but 1975 was cloudy and had the lowest July-August means. Extreme variability also occurred over short (1-3 day) periods. The maximum and minimum daily totals for the 1974 season occurred on two consecutive days

Figure 23. Environmental data from Site 2 for 1973.

a. Daily irradiance; indicated are means for months or portions (dashed line and circles).

b. Mean daily air (shelter) temperature; indicated are monthly means and absolute temperatures (dashed lines and circles).

c. Mean daily (shelter) vapor pressure deficit (VPD); indicated are monthly means and absolute maxima (dashed lines and circles).

d. Precipitation; indicated are individual events, trace amounts (bars below the line), measurement period (arrows), and snow (s).

e. Wind speed at 60 cm; indicated are daily means (solid lines), periods greater than one day (dotted lines), and monthly or interval means (dashed line and circles).

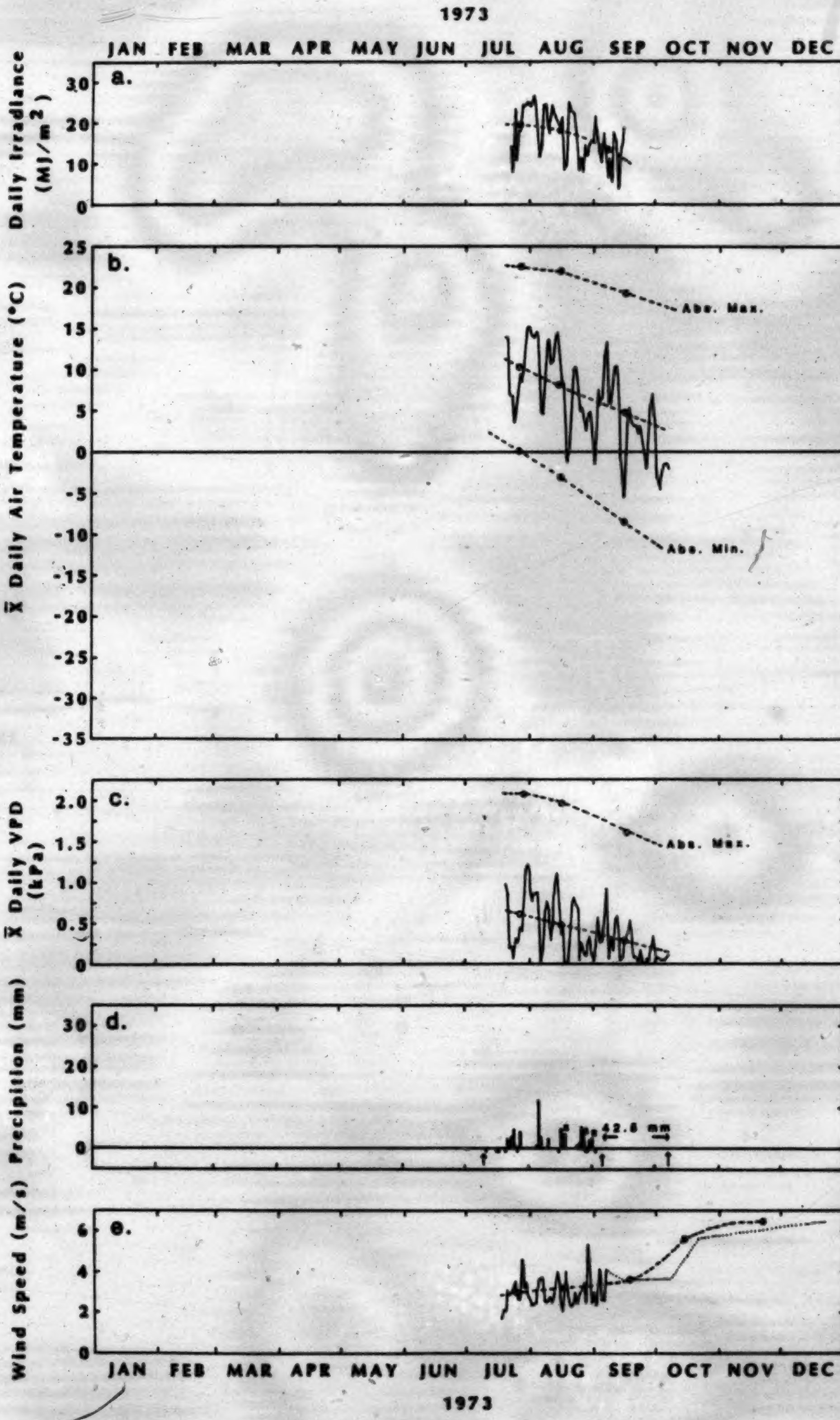

1973
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
a.
Daily Irradiance (MJ/m²)
0 10 20 30
b.
X̄ Daily Air Temperature (°C)
-35 -30 -25 -20 -15 -10 -5 0 5 10 15 20 25
Abs. Max.
Abs. Min.
c.
X̄ Daily VPD (kPa)
0 0.5 1.0 1.5 2.0
Abs. Max.
d.
Precipitation (mm)
0 10 20 30
42.6 mm
e.
Wind Speed (m/s)
0 2 4 6
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1973

Figure 24. Environmental data from Site 2 for 1974.

a. Daily irradiance; indicated are means for months or portions (dashed line and circles).

b. Mean daily air (shelter) temperature; indicated are data extrapolated from Site 1 (dotted line), and monthly means and absolute temperatures (dashed lines and circles).

c. Mean daily (shelter) vapor pressure deficit (VPD); indicated are data extrapolated from Site 1 (dotted line), and monthly means and absolute maxima (dashed lines and circles).

d. Precipitation; indicated are individual events, trace amounts (bars below the line), measurement period (arrows), and snow (s).

e. Wind speed at 60 cm; indicated are daily means (solid lines), periods greater than one day (dotted lines), and monthly or interval means (dashed line and circles).

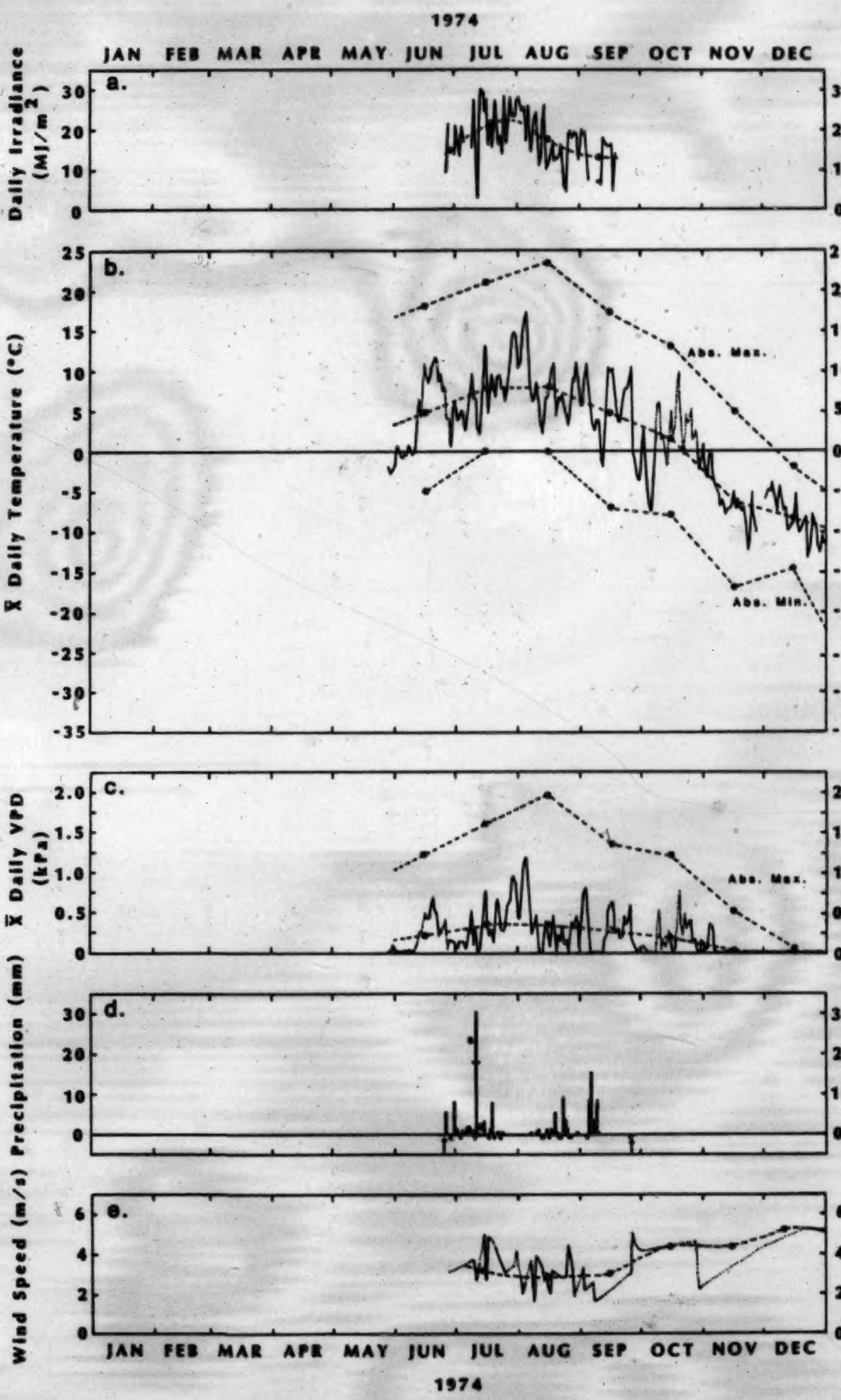

1974
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
a.
Daily Irradiance (MJ/m^2)
0 10 20 30
b.
$\bar{X}$ Daily Temperature (°C)
25 20 15 10 5 0 -5 -10 -15 -20 -25 -30 -35
Abs. Max.
Abs. Min.
c.
$\bar{X}$ Daily VPD (kPa)
0 0.5 1.0 1.5 2.0
Abs. Max.
d.
Precipitation (mm)
0 10 20 30
e.
Wind Speed (m/s)
0 2 4 6
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1974

Figure 25. Environmental data from Site 2 for 1975.

a. Daily irradiance; indicated are means for months or portions (dashed line and circles).

b. Mean daily air (shelter) temperature; indicated are data extrapolated from Site 1 (dotted line), and monthly means and absolute temperatures (dashed lines and circles).

c. Mean daily (shelter) vapor pressure deficit (VPD); indicated are data extrapolated from Site 1 (dotted line), and monthly means and absolute maxima (dashed lines and circles).

d. Precipitation; indicated are individual events, trace amounts (bars below the line), measurement period (arrows), and snow (s).

e. Wind speed at 60 cm; indicated are daily means (solid lines), periods greater than one day (dotted lines), and monthly or interval means (dashed line and circles).

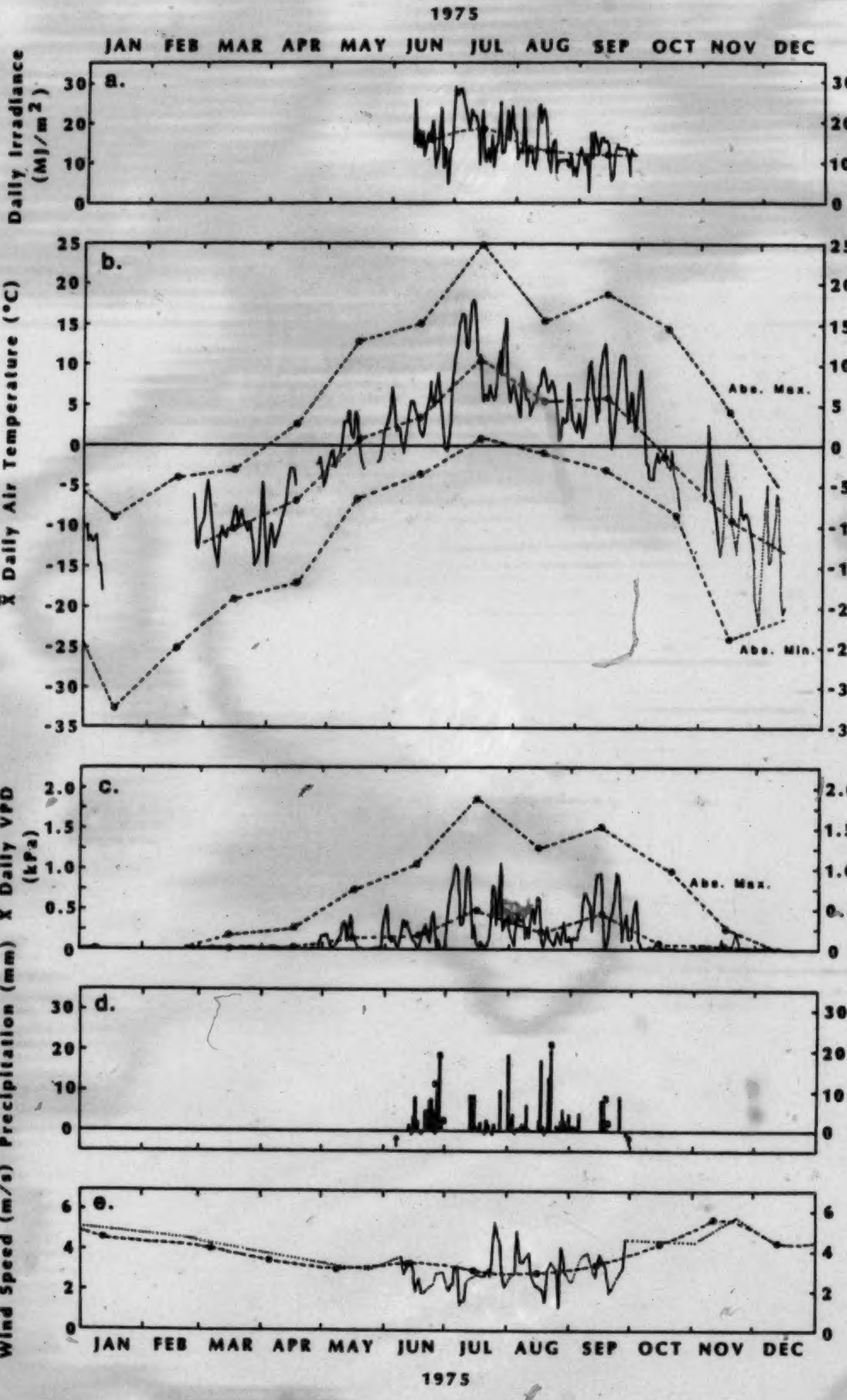

1975
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
a.
Daily Irradiance (MJ/m^2)
0 10 20 30
b.
$\bar{X}$ Daily Air Temperature (°C)
25 20 15 10 5 0 -5 -10 -15 -20 -25 -30 -35
Abs. Max.
Abs. Min.
c.
$\bar{X}$ Daily VPD (kPa)
0 0.5 1.0 1.5 2.0
Abs. Max.
d.
Precipitation (mm)
0 10 20 30
e.
Wind Speed (m/s)
0 2 4 6
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
1975

Table 10. Monthly summary of environmental data from Site 2 for 1973, 1974, and 1975. (n) = days of record per month or inclusive dates for each parameter.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1973												
Global Radiation (MJ•m^{-2}•d^{-1})							(22-31)	month	(1-15)			
$\bar{X}$ Daily Irradiance							19.1	17.9	13.1			
Max. Daily							25.1	26.6	21.7			
Min. Daily							7.9	7.7	3.2			
Temperature (°C)							(19-31)	month	month			
$\bar{X}$ Daily							10.3	8.0	4.2			
Abs. Max.							22.5	22.0	19.5			
$\bar{X}$ Daily Max.							15.5	13.1	7.9			
$\bar{X}$ Daily Min.							5.4	3.8	0.8			
Abs. Min.							0	-3.0	-8.5			
Vapor Pressure Deficit (kPa)							(19-31)	month	month			
$\bar{X}$ Daily							0.60	0.47	0.25			
Abs. Max.							2.06	1.96	1.61			
Precipitation (mm)							(11-31)	month				
Monthly (Period) Total							15.0	43.3				
Days with measurable ppt.							6	13				
Summer Period:							(July 11-Sept. 5)					
% of days with measurable ppt.							33%					
% of days with trace ppt.							16%					
% of ppt. as snow							19%					
Windspeed (m/s)							(17-31)	month	month	month	month	
$\bar{X}$ Daily							3.0	3.2	3.5	5.6	6.5	
1974												
Global Radiation (MJ•m^{-2}•d^{-1})							(28)	month	(16)			
$\bar{X}$ Daily Irradiance							21.3	17.3	13.2			
Max. Daily							30.1	28.1	20.0			
Min. Daily							3.2	4.1	4.4			
Temperature (°C)						month	month	month	month	month	(1-26)	month
$\bar{X}$ Daily						4.2	7.7	8.0	4.7	1.5	-6.2	-8.4
Abs. Max.						18.0	21.0	23.5	17.0	13.1	5.0	-2.0
$\bar{X}$ Daily Max.						8.0	12.2	12.5	8.1	3.5	-4.4	-7.2
$\bar{X}$ Daily Min.						1.6	3.4	4.3	1.3	-1.2	-7.9	-9.6
Abs. Min.						-5.0	0	0	-7.0	-8.0	-17.0	-14.5

Table 10. (continued)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Vapor Pressure Deficit (kPa)						month	month	month	month	month	(1-28)	month
$\bar{X}$ Daily						0.22	0.37	0.34	0.27	0.19	0.04	0.01
Abs. Max.						1.22	1.67	1.97	1.36	1.22	0.54	0.07
Precipitation (mm)						(25-30)	month	month	(1-26)			
Monthly (Period) Total						13.7	53.8	27.2	37.2			
Days with measurable ppt.						2	15	12	6			
Summer Period							(June 25-Sept. 26)					
% of days with measurable ppt.							37%					
% of days with trace ppt.							17%					
% of ppt. as snow							10%					
Wind speed (m/s)							month	month	month	month	month	month
$\bar{X}$ Daily							3.2	2.9	3.1	4.4	4.4	5.2
							1975					
Global Radiation ($MJ \cdot m^{-2} \cdot d^{-1}$)						(10-30)	month	month	(1-27)			
$\bar{X}$ Daily Irradiance						15.2	18.5	12.9	12.0			
Max. Daily						25.3	28.6	24.5	17.3			
Min. Daily						4.7	9.0	6.6	2.5			
Temperature (°C)	month	month	month	(1-14, 25-30)	(1-18, 25-31)	month	month	month	month	(1-21)	(2-30)	(1-12)
$\bar{X}$ Daily			-10.3	-6.8	0.7	3.4	10.6	5.5	6.0	-1.5	-9.3	-12.2
Abs. Max.	-8.5	-3.5	-3.0	2.5	13.0	15.0	25.0	15.5	19.0	14.0	4.0	-4.0
$\bar{X}$ Daily Max.			-8.0	-3.7	3.9	6.7	15.4	8.9	10.2	-0.1	-7.5	-10.4
$\bar{X}$ Daily Min.			-12.5	-9.7	-2.2	0.5	6.1	2.7	2.4	-3.1	-11.0	-14.3
Abs. Min.	-33.0	-25.0	-19.0	-17.0	-6.5	-3.5	1.0	-1.0	-3.0	-8.5	-24.0	-21.5
Vapor Pressure Deficit (kPa)			month	(1-14, 25-30)	(1-18, 25-31)	month	month	month	month	(1-21)	(2-30)	(1-12)
$\bar{X}$ Daily			0.01	0.03	0.13	0.16	0.49	0.21	0.43	0.06	0.03	0.01
Abs. Max.			0.17	0.25	0.74	1.06	1.88	1.26	1.51	0.96	0.27	0.04
Precipitation (mm)						(7-30)	month	month	month			
Monthly (Period) total						70.1	40.0	107.3	30.9			
Days with measurable ppt.						11	10	22	[illegible]			

Table 10. (continued)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Summer Period						(June 7-Sept. 30)						
% of days with measurable ppt.							35%					
% of days with trace ppt.							7%					
% of ppt. as snow							23%					
Windspeed (m/s)	month	month	month	month	month	month	month	month	month	month	month	month
$\bar{X}$ Daily	4.6	4.4	4.1	3.5	3.1	3.3	3.0	3.0	3.3	4.4	5.6	4.4

in July.

Air Temperature

Maximum air temperatures coincided with the period of maximum radiation in July. Mean daily temperatures at this time were ca. 10°C, and mean daily maximum and minimum temperatures deviated 4-5°C from this. Absolute maximum temperatures were normally ca. 22-23°C, but 25°C was recorded in July, 1975, during a period of above normal monthly temperatures at Jasper townsite. Freezing temperatures can occur at any time during the summer near treeline. Absolute minimum temperatures from +1 to -3°C were recorded in July and August of all three years, and -3.0 to -8.5°C in June and September. Mean daily temperatures began to rise above 0°C in May and dropped below again in late September. Absolute temperatures exceeded 0°C during the April-November period, but temperatures were continuously below 0°C from December through March. Absolute minimum temperatures <-20°C were recorded from November through February, with January the coldest month. Extreme monthly temperature variations of ca. 22-24°C occurred during the summer months or in January-February, due to extreme cold spells. March-May was the least variable period with extreme ranges ca. 16-20°C. Diurnal fluctuations were greatest during the summer months, and conversely, winter temperatures were diurnally more stable.

Mean daily temperatures on Signal Mountain averaged 5.9°C lower than at Jasper townsite for the March-December period (incomplete January-February data). The greatest difference occurred during April-June ($\bar{X}_{\Delta}T$ = -8.3°C) when the snow at higher elevations served as a heat sink during snowmelt while Jasper townsite was essentially snow free at the time. Differences were less during July-September ($\bar{X}_{\Delta}T$ = -6.0°C) and were lowest during the winter ($\bar{X}_{\Delta}T$ = -4.5°C). Maximum monthly temperatures averaged 9.8°C lower than at Jasper townsite for the year. Monthly differences ranged from a low of 6.7°C in November, 1974, to a high of 15.8°C in April, 1975. Differences were generally lowest during the July-October period and highest during October-June. Minimum monthly temperatures were lower on Signal Mountain during the April-October period ($\bar{X}_{\Delta}$Tmin = -2.2°C) but higher during the winter ($\bar{X}_{\Delta}$Tmin = +5.2°C) when cold air was trapped in valleys. Throughout the year the alpine climate was thermally less variable than at Jasper townsite.

The elevationally correlated temperature differences between Site 2 and Jasper were also reflected in the differences between study Sites (Table 11). Temperatures near treeline were consistently higher than at Site 2 but monthly variability was high. The 1973 data provides a comparison between the primary communities at each study Site. The C. mertensiana community at Site 1 had slightly higher temperatures than Site 2, but differences were not significant considering hygrothermograph error (± 0.5°C), However, mean daily maximum temperatures in August-September, 1973, averaged 1.3°C higher at Site 1.

Table 11. Temperature and VPD (shelter) differences at Site 1 as compared with Site 2. Comparisons based on daily values. n = number days per month, N.S. = no significant difference, CI.95 indicted. Site 1 shelter at 2 m from December 1974 through May 1975.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1973												
							n=13	n=31	n=30	n=6		
Temperature (˚C)												
$\bar{X}$ Daily Max.							N.S	+1.3±0.3	+1.3±0.3	N.S.		
$\bar{X}$ Daily							N.S.	N.S.	N.S.	N.S.		
$\bar{X}$ Daily Min.							N.S.	N.S.	N.S.	N.S.		
Vapor Pressure Deficit (kPa)												
Abs. Max.							+0.01	-0.07	+0.01	N.S.		
$\bar{X}$ Daily							N.S.	N.S.	N.S.	N.S.		
1974												
					n=4	n=21	n=31	n=30		n=9		n=26
Temperature (˚C)												
$\bar{X}$ Daily Max.					N.S.	N.S.	+1.5±0.3	+1.2±0.3		+1.4±0.8		+2.0±0.4
$\bar{X}$ Daily					N.S.	-1.0±0.2	N.S.	N.S.		N.S.		+1.4±0.4
$\bar{X}$ Daily Min.					N.S.	N.S.	N.S.	N.S.		N.S.		+0.9±0.4
						n=23						
Vapor Pressure Deficit (kPa)												
Abs. Max.						-0.28	+0.26	+0.32				+0.08
$\bar{X}$ Daily					+0.10±.07	+0.07±.03	+0.07±.02	+0.06±.01		N.S.		N.S.
1975												
	n=9	n=6	n=24	n=18	n=24	n=30	n=23	n=28	n=18	n=11	n=11	
Temperature (˚C)												
$\bar{X}$ Daily Max.	N.S.	+4.1±1.0	+4.1±0.7	+6.9±1.1	+5.0±1.0	+2.2±0.6	+2.0±0.4	+1.6±0.2	+1.2±0.6	+1.1±0.3	N.S.	
$\bar{X}$ Daily	N.S.	+2.7±0.8	+1.9±0.6	+4.1±0.9	+3.5±0.6	+1.9±0.3	+1.8±0.3	+1.1±0.1	+1.1±0.6	N.S.	N.S.	
$\bar{X}$ Daily Min.	N.S.	+2.3±1.5	N.S.	+4.1±0.9	+3.4±0.6	+1.9±0.3	+1.8±0.3	+1.1±0.1	+1.1±0.5	N.S.	N.S.	
Vapor Pressure Deficit (kPa)												
Abs. Max.	+0.10	+0.20	+0.11	+0.59	+0.43	+0.26	+0.10	+0.13	-0.03	+0.07	+0.12	
$\bar{X}$ Daily	N.S.	N.S.	+0.05 ±.02	+0.18 ±.07	+0.16 ±.05	N.S.	N.S.	+0.03 ±.01	N.S.	+0.04 ±.02	N.S.	

Shelter relocation in 1974 provided a comparison between more exposed microsites at Sites 1 and 2. Mean daily maximum temperatures in 1974 were again significantly higher at Site 1 (1.2-1.5°C). Temperature differences were much greater in 1975. Temperatures averaged 1-2°C higher at Site 1 during the summer months and from 3-7°C higher during the late winter and spring months. This latter difference may be due to shelter location and not Site differences. During the December 1974-May 1975 period the shelter at Site 1 was located at 2 m to avoid drifting snow, and temperature stratification may have occurred near the snow surface. Winter diurnal temperature fluctuations were greater at Site 1, and extreme monthly minimums were 2-4°C lower.

Vapor Pressure Deficit

Vapor pressure deficits were directly correlated with temperature and were highest during the summer months or the warmest periods of the day. Maximum VPD's in July-August were *ca*. 1.9-2.0 kPa, and in June, September, and October were *ca*. 1.0-1.6 kPa. Maximum VPD's were much lower during spring and fall (0.7-1.2 kPa) and were very low in mid winter (<0.1 kPa). Mean daily VPD's, calculated over monthly periods, show the influence of precipitation and frequency of cloud cover. July, 1973, had the highest mean daily VPD's (0.60 kPa) during a month of extreme precipitation deficit at Jasper townsite. The lowest mean daily VPD's recorded during the July-August period (0.21 kPa in August, 1975) occurred during a month of below-normal temperatures and above-normal precipitation. September, 1975, had mean daily VPD's (0.43 kPa) more typical of the hotter summer months due to above-normal temperatures and below-normal precipitation. These conditions could influence the water budget of Cassiope going into winter. Mean daily VPD's were low (generally <0.05 kPa) during winter due to low temperatures and high relative humidities.

Between Site differences in VPD's were related to temperature differences (Table 11). Site differences were higher in 1974 and 1975 than in 1973. Maximum monthly VPD's were generally higher at Site 1, but during some months were lower. Maximum VPD's averaged 0.13 kPa higher at Site 1 during July-August, but winter differences were less. The greatest differences in maximum (0.43-0.59 kPa) and mean daily (ca. 0.17 kPa) VPD's were recorded in April-May, 1975, and were probably related to differences in shelter height. Differences in mean daily VPD's were not significant or generally small (<0.08 kPa) throughout the rest of the year.

Summer Precipitation

Summer precipitation on Signal Mountain showed great daily, monthly, and yearly variability. Mean monthly totals for July-August for the three years (excluding July, 1973) were 55 mm, but ranged from a high of 107 mm in August, 1975, to a low of 27 mm in August, 1974. Totals for July, 1973, were probably less than 20 mm. Summer precipitation was lowest in 1973 (101 mm between 1 July-7 October) and highest in 1975 (253 mm between 7 June-30 September).

Measurable precipitation occurred with a frequency of 1 day in 3 and was consistent between years (33%-37% of days during record period). When trace amounts are included, precipitation occurred with a frequency of 1 day in 2. This is indicative of the frequency of summer cloud cover and storms. The maximum daily totals exceed 30 mm in July, 1974, and exceeded 15 mm on four days during June-August, 1975. Periods of 7-13 consecutive days without measurable precipitation were recorded in July and August of all three years. The longest dry period was 17 days in September, 1974. An average of 17% of the summer precipitation occurred as snow (does not include "mixed" precipitation), but the years were variable (10% in 1974 to >24% in 1975).

Precipitation events on Signal Mountain were generally correlated with similar events at Jasper townsite. Only rarely (approximately 2-4 days per summer) did measurable precipitation occur on either Signal Mountain or at Jasper townsite without at least trace amounts being recorded at the other location. Summer precipitation at Jasper townsite (June-September) for 1973, 1974, and 1975 averaged 58%, 76%, and 102%, respectively, of the 1926-1975 record. Summer precipitation on Signal Mountain during the measurement periods averaged 123% of Jasper townsite, but varied from 105% in 1974 to 134% in 1975. Not only was summer precipitation higher in the alpine zone, but a greater proportion occurred as snow.

Summer precipitation differences between Sites were not great and probably reflect microsite variability and wind patterns around collectors rather than any real site differences. Precipitation at Site 1 averaged 102% of Site 2 for the 3 year period, but varied from a low of 95% in 1974 to a high of 115% in 1973.

Wind

The alpine zone of Signal Mountain is a moderately windy environment, particularly on the windward southerly slopes and along the summit ridge. High winds can occur in all but the most protected Cassiope habitats, but with reduced frequency and duration. Winds showed great temporal variability, both seasonally and over short periods (hourly to daily). The maximum daily winds tended to occur during afternoons and minimums at night or early morning, but this was not quantified. Wind directions were recorded only at time of anemometer readings (ca. 1800 h MST). The predominant wind directions were WSW varying to S or W, and occasionally to N, and only rarely to E. This is consistent with the more detailed observations of Hrapko and La Roi (1978).

Wind speeds are reported from the exposed Dryas-lichen community at Site 2 where anemometer placement was dictated by winter snow cover. Wind speeds were lowest during the April-September period (2.9-3.5 m/s) and highest during October-March (4.1-6.5 m/s). Mean daily wind speeds were ca. 3 m/s in July-August of the three years. Maximum and minimum mean daily wind speeds during this period were *ca*. 5.0-5.5 m/s and 1.2-1.6 m/s, respectively. Winds consistently increased in fall, and winter wind speeds averaged 161% of August values. Mean wind speeds for the winter months generally exceeded maximum daily values recorded during summer.

Wind profiles were not measured in winter but observations suggest less attenuation of wind near the surface than in summer. Microtopographic irregularities are eliminated in winter and surface friction is reduced. Exposed plants projecting above the snowpack experience much higher winds (both absolute and relative to 60 cm height) than during summer. Wind speeds are difficult to assess or are even meaningless in all but the most exposed *Cassiope* habitats during winter because of snow accumulations.

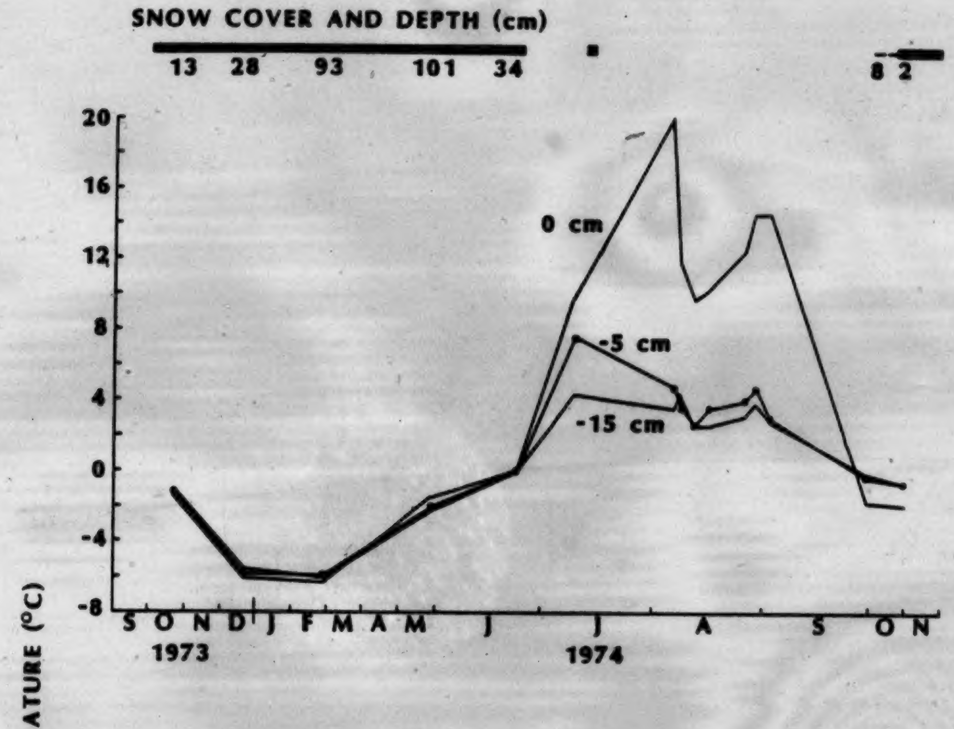
Comparisons of relative wind speeds at different microsites are given in Table 12. These comparisons are based on wind totals over the entire period, but comparisons based on individual measurement periods are similar (and significant at $P<0.01$). *Cassiope tetragona* microsites were windier than *C*. *mertensiana* microsites and in general, Site 2 was windier than Site 1. The anomalous high relative wind speeds at the Site 1 *C*. *tetragona* community were due to anemometer placement to avoid drifting snow, and the location was slightly more exposed than was typical of *C*. *tetragona* at this Site.

Table 12. Relative wind speeds at different microsites.

Site	Microsite	Relative Wind	Days of Comparisons With Other Sites
2	_Dryas_-lichen	1.00	670
1	_C. tetragona_	0.78	615
2	_C. tetragona_	0.71	201
2	_C. mertensiana_	0.64	2
1	_C. mertensiana_	0.57	144

Soil Temperatures

Soil temperatures at selected depths in the _C. tetragona_-_Dryas_ community at Site 2 (20 m along transect) are shown in Fig. 26. Maximum temperatures in surface horizons occurred during July and coincided with maximum air temperatures and radiation. Summer temperatures at 0 cm (beneath 1-2 cm of litter) averaged 2-5°C below ambient, although extremes of 0.5°C above and 15°C below (following snow melt) were recorded. Midday temperatures at -5 to -15 cm varied between 3°C and 8°C. Maximum temperatures at -50 cm were <4°C and occurred in mid August. Soil temperatures dropped below 0°C in late September, paralleling the decline in mean daily air temperatues. Minimum soil temperatures occurred in February-March, one to two months after the occurrence of minimum air temperatues. Minimum soil temperatures at all depths were -6 to -8°C. Soil temperatures increased to -1 to -2°C about one month prior to snow melt. Temperatures increased gradually for about two weeks following snow release under the influence of melt



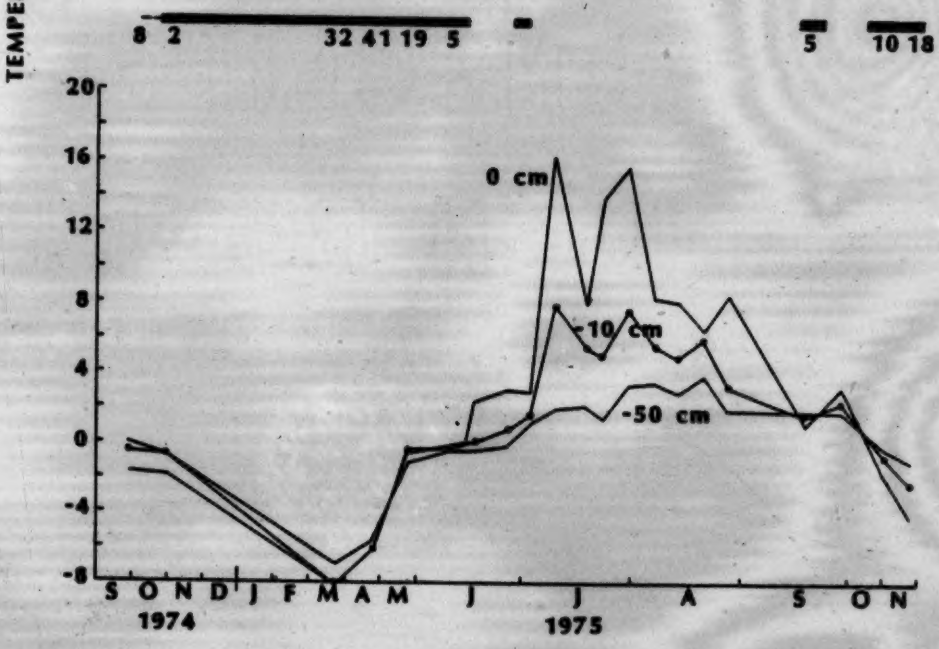


Figure 26. Soil temperatures during 1974 and 1975 at the Site 2 C. *tetragona*-*Dryas* community. Note soil depths differ between years; snow cover is indicated.

waters. Seasonal fluctuations in soil temperatures were greater in 1975 than in 1974 due to higher air temperatures in July, lower air temperatures in mid winter, and a below-normal snow pack.

Seasonal soil temperature fluctuations were reduced in all other Cassiope communities from that reported above. Summer soil temperatures at the Site 2 C. tetragona-late snow release community were about 2°C higher, due primarily to less plant cover. Winter soil temperatures were about 3°C higher due to greater snow accumulations. Summer soil temperatures at the Site 1 C. tetragona community were about 0.5°C higher at 0 cm. However, conditions were more isothermal throughout the rest of the profile; temperatues were 2°C lower at -10 cm and 2°C higher at 50 cm. Winter soil temperatures were about 4°C higher at all depths.

Soil temperatures were seasonally more stable and profiles more isothermal in all C. mertensiana communities. Soils of C. mertensiana communities were 2-4°C cooler during the summer months and 1.5-4.5°C warmer during the winter months than the C. tetragona communities at the respective Sites. Soils of C. mertensiana communities remained around -1 to 0°C for approximately one month longer prior to snow release than the adjacent C. tetragona communities. However, soil temperatures increased more rapidly after snow release to mid summer maxima. The Site 1 C. mertensiana community was about 1°C warmer at 0 cm during the summer, 1°C cooler at -10 to -50 cm during the summer, and about 1°C warmer at all depths during the winter than the *C. mertensiana* community at Site 2.

The slightly higher soil surface temperatures at Site 1 were related to slightly higher air temperatures at lower elevations. The reduced magnitude of seasonal temperature fluctuations in the *C. mertensiana* communities was due to greater plant cover, soil moisture, soil organic matter, and snow accumulations.

Profiles

Cassiope plants experience small but consistent microenvironmental differences due to the relative exposure of microsites and density of plant canopies. Figure 27 compares near surface microenvironments at adjacent Site 1 *Cassiope* microsites on 20 August 1973. This was a typical, warm, dry, late summer day; daily irradiance was 22.8 $MJ \bullet m^{-2} \bullet d^{-1}$, mean daily shelter temperature was 7.5°C, mean daily shelter VPD was 0.64 kPa, and mean daily windspeed at 60 cm was 1.28 m/s.

Air temperatues within the plant canopies at 5 cm were frequently 2-4°C higher than in the ambient air at 100 cm. Differences were greater within the *C. mertensiana* canopy. Soil temperatures beneath *C. tetragona* were up to 5°C higher at 0 cm and about 1°C higher at -15 cm than beneath *C. mertensiana*. Daily temperature fluctuations were reduced at -15 cm. Differences in leaf and air temperatures were also noted. *Cassiope* leaf temperatures were elevated considerably above ambient and differences were greater with *C.*

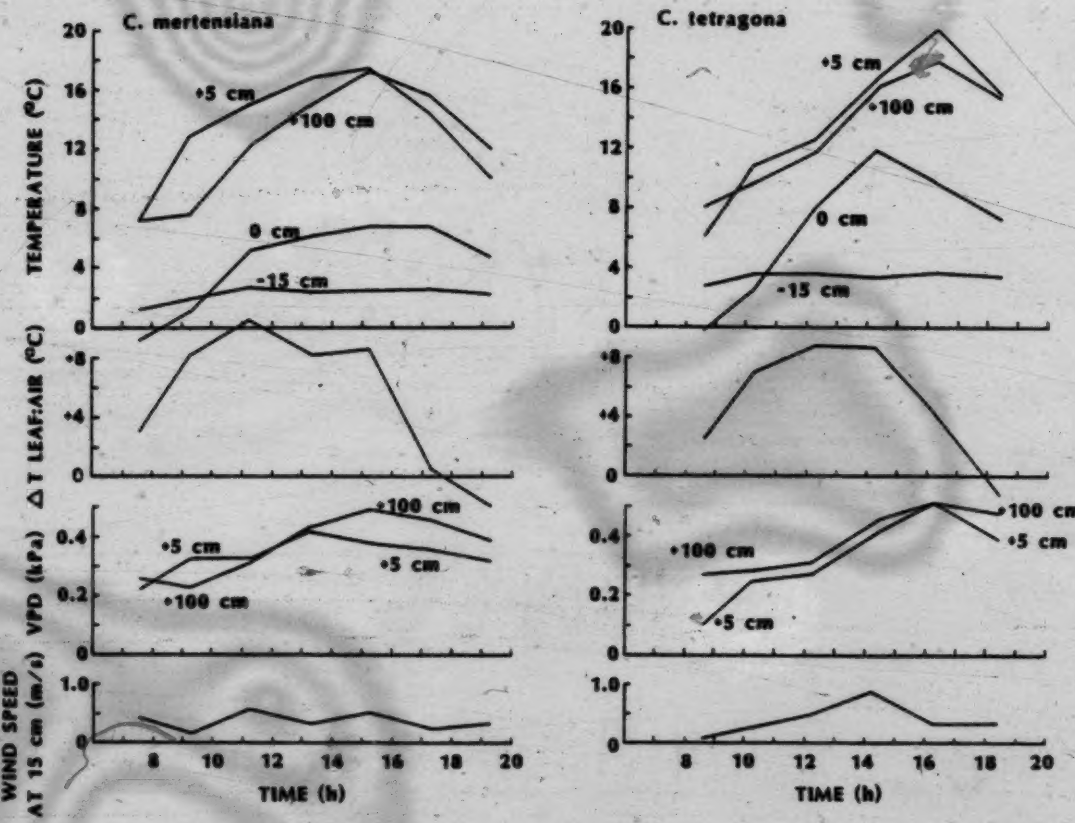


Figure 27. Near surface microenvironments at Site 1 Cassiope spp. microsites on 20 August 1973.

mertensiana. The subambient leaf temperatures reported are probably an artifact of measurement technique as transpiration rates are to low to result in this degree of evaporative cooling. However, this does not invalidate the trend, only the absolute magnitude of the leaf temperature elevation. Differences in VPD profiles were small. Vapor pressure deficits within plant canopies tended to be lower than in the ambient air, even though canopy air temperatures were higher. Windspeeds were low and relative constant during the day in the C. mertensiana microsite, but showed a typical late afternoon peak in the C. tetragona microsite. Figure 28 shows wind profiles from the summed data for all measurement periods. Cassiope tetragona microsites were windier than adjacent C. mertensiana microsites, and Site 2 was windier than Site 1. Differences within plant canopies are significant. These results are similar to those recorded at 60 cm with three-cup anemometers at the respective microsites (Table 12). Differences in windspeeds and air mixing within plant canopies are largely responsible for the air and leaf temperature differences noted above.

Similar results were recorded on other measurement days of high radiation and temperatures. On cool, cloudy days, air and soil temperatures and VPD's were lower and both daily changes and microsite differences reduced.

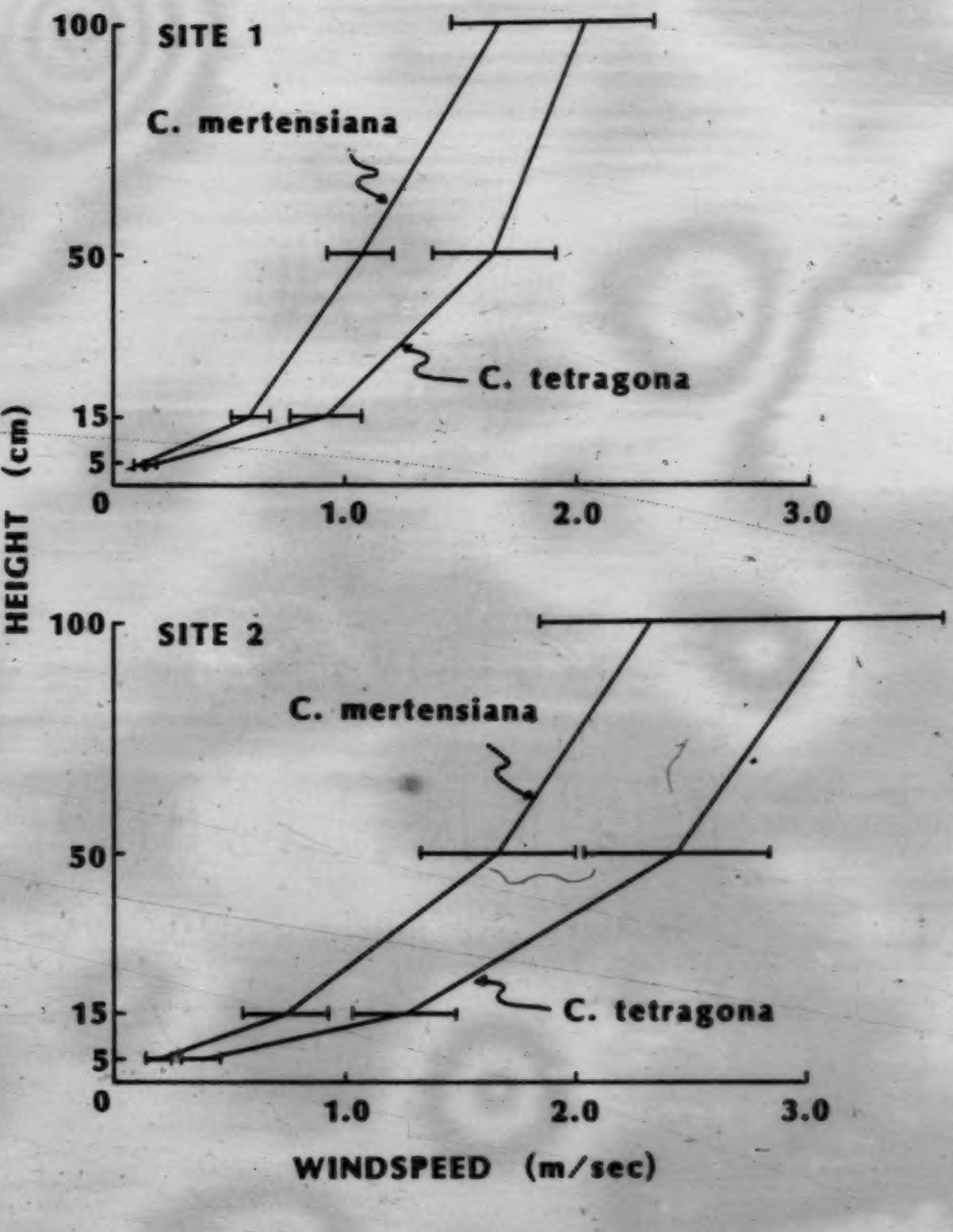


Figure 28. Wind profiles above _Cassiope_ plants at Sites 1 and 2. CI.95 are indicated.

IV. PLANT RESPONSES

A. Phenology and Growth

a. Methods

Initial observations indicated that general growth responses and phenology of _Cassiope_ were highly variable and related to date of snow release as influenced by elevation and microsite conditions. This agrees with Holway and Ward (1963, 1965) who considered snow cover and the retarding influence of cold meltwater on soil temperature as the primary factors influencing phenology of alpine plants in Colorado. _Cassiope_ in exposed microsites near treeline (roadsides, base of trees, etc.) often melted out 4-8 wk ahead of those in late snowbank microsites at higher elevations, and phenological events were correspondingly advanced. This variability was more pronounced with _C. tetragona_ as it occupied a wider range of habitats. Observations were thus concentrated at the two intensive study Sites as they represented the "normal" habitats of both species. _Cassiope mertensiana_ at Site 1 and _C. tetragona_ at Site 2 occupied a wider range of habitats than the alternate species at each Site. Thus, microsites could be selected representing early, mid, and late snow release for _C. mertensiana_ at Site 1 and _C. tetragona_ at Site 2 and these could be compared with one microsite for each species at the alternate Site.

Phenological observations and measurements of shoot elongation were conducted from 1973 through 1975 (the 1973 data are incomplete and therefore not reported). Plants located in a homogeneous area were marked in a grid pattern (1.5 m spacing) in mid July, 1973, and phenological observations concentrated on these (Table 13). Five vigorous shoots, unbranched near the apex, were randomly selected from within the canopy of each plant and marked for measurements of shoot elongation. A leaf was clipped 10.0 mm below the apex and measurements of shoot length taken with a fine scaled ruler. Measurements were taken at snow release and at approximately weekly intervals throughout the summers of 1974 and 1975. Shoot senescence and mortality related to microtine grazing (particularly in C. mertensiana late snow release microsites), mechanical breakage, or desiccation, reduced sample size and these shoots were eliminated from the data analysis. To complement and expand the data base, additional plants were marked and sampled in 1975 along a snow release gradient at Sites 1 and 2.

Additional shoots of C. tetragona were collected in 1974 for a chronological sequencing of shoot growth and leaf and flower production. Many shoots flower yearly and pedicels remain attached, allowing successive years growth intervals to be distinguished. This is more prevalent in the vigorous, protected leeward shoots at the base of the plant canopy. Growth and production of such shoots would represent a near maximum and not be directly comparable with the

Table 13. Sampling regime for phenological observations and measurements of shoot elongation at selected microsites.

Site	Microsite	Snow Release	Number of Marked Plants	Observation Years
1	C. mertensiana	mid	10	1974-75
	C. mertensiana	late	"	"
	C. tetragona	mid	20	"
2	C. mertensiana	mid	"	"
	C. tetragona	mid	"	"
5	C. tetragona	mid	"	"
1	C. mertensiana	early	5	1975
	C. mertensiana	mid	"	"
	C. mertensiana	late	"	"
	C. tetragona	mid	"	"
2	C. mertensiana	mid	"	"
	C. tetragona	early	"	"
	C. tetragona	mid	"	"
	C. tetragona	late	"	"

"average" canopy shoots as marked for measurements of shoot elongation. Samples were collected from early, mid, and late snow release microsites at Site 2. Cassiope mertensiana was not analyzed in this fashion due to a more irregular pattern of flowering and branching which complicated shoot chronologies, particularly in late snow release microsites.

b. Results

Phenology

The yearly sequence of phenophases in C. mertensiana and C. tetragona is similar although the timing differs. At growth cessation in the fall, shoot segments and leaves that will elongate to full size the following summer are already fully formed, partially expanded, and grouped in a tight cluster around the shoot apex, partially enveloped by the proximal leaves of the current year. Flower buds are also partially expanded, but to a greater degree in *C. mertensiana*. Leaf and bud primordia that will expand to full size two years later are also present on the shoot apex. No elongation or expansion of flower buds or shoots occurs during the winter months. At spring snow release, flower buds of *C. mertensiana* (and occasionally *C. tetragona* in late snow release microsites) have noticeably swelled from the fall condition, bulging out the enclosing leaves. The perception of light penetrating the snow, or an interaction with temperature, may be involved in this response (see Richardson and Salisbury 1977). Flower bud expansion continues in the spring, often before any noticeable shoot elongation. When flower buds near 100% expansion, pedicels begin to elongate and flowering commences. Peak flowering usually lasts only a few days on a single plant, but a few flowers may be produced over a 2-3 wk or longer period. Most shoot elongation occurs during the period of flowering and early capsule swelling. Near the end of the period of maximum shoot elongation (*ca*. mid August), yellowing and senescence of the oldest leaves occurs in *C. tetragona*. Leaf senescence in *C. mertensiana* is not as noticeable, and probably extends over a much longer period. Old leaves remain attached to living stems and decompose *in situ*. Capsule swelling and elevation often begins before corollas are dropped. Ovule ripening continues after the capsules are fully swelled. Capsule dehiscence and seed dispersal begins *ca*. mid September; prior to continuous fall snow cover.

Phenological patterns of *Cassiope* at various microsites in 1974 and 1975 are shown in Fig. 29. Snow release in 1975 occurred earlier than in 1974 (see Snow Cover Section), microsite differences in dates of release were condensed, and phenological events were advanced. Flower bud expansion in *C*. *tetragona* began either *ca*. June 15-20 or approximately one week after snow release (except at Site 2 late snow release microsite in 1975) and was probably limited by low temperatures during early June in early snow release microsites. Late spring snow storms in 1974 and 1975, resulted in two and six days snow cover, respectively, in *C*. *tetragona* microsites. This may have slightly delayed the onset of flowering. However, flower bud expansion appeared to proceed unimpeded beneath the snow. Flower bud expansion in *C*. *mertensiana* was initiated prior to snow release at all microsites and overlapped with both the periods of *C*. *tetragona* flower bud expansion and maximum seasonal temperatures in July.

The initiation of flowering and period of peak flowering in *C*. *tetragona* occurred earlier in the season than in *C*. *mertensiana*. However, peak flowering in *C*. *tetragona* was delayed, relative to snow release, due to

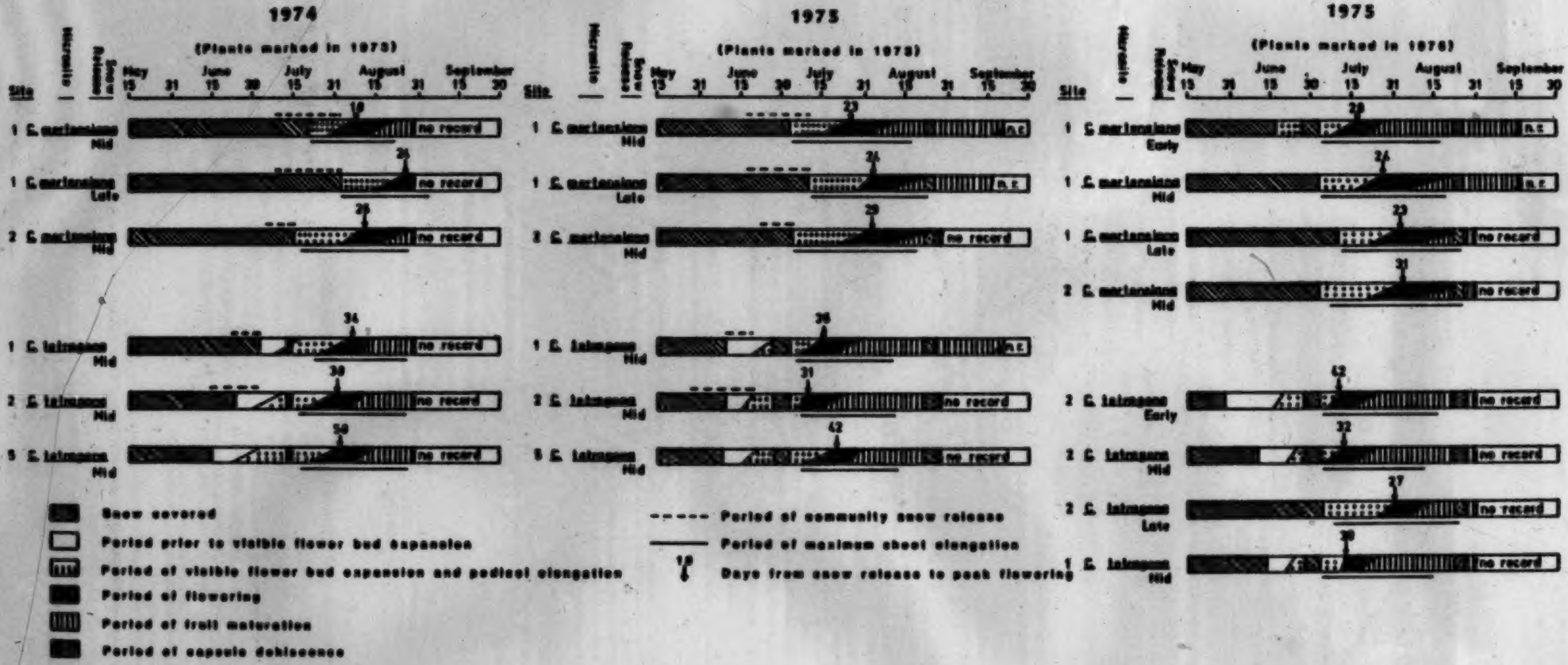


Figure 29. Phenological patterns of Cassiope at various microsites in 1974 and 1975. Included are plants marked in 1973, and additional plants marked along a snow-release gradient in 1975 (see Table 13).

the early season period of inactivity. Also, there was a tendency for flowering in both species to be delayed, relative to snow release, at higher elevation microsites. Peak flowering in C. mertensiana and C. tetragona occurred 18-31 and 27-48 days after snow release, respectively. Plants of both species that melted out on similar dates at the same Sites (marked along snow release gradient in 1975) showed similar patterns of flower bud expansion, initiation of flowering, and peak flowering. This indicates that the initial period of inactivity in early snow released C. tetragona may not be obligatory, but related to unfavorable early season environmental conditions. Although peak flowering was asynchronous in the two species, some overlap of flowering periods occurred. Thus, cross pollination is not prevented by the timing of flowering periods. Flowering in C. mertensiana tended to extend over a longer period, especially in plants of late snow release. Reproductive development was not linked to shoot elongation (Fig. 29).

The period of capsule swelling and fruit maturation began earlier in C. tetragona, but extended through August and early September in both species. The timing of fruit dehiscence was not observed in all years and microsites, but generally began in mid September. Fruit maturation and seed production were reduced in plants (especially C. mertensiana) of late snow release and flowering.

Shoot Elongation

Shoot elongation (growth) was essentially synchronous in both species, except where delayed by late snow release (Fig. 30 and Table 14). Plants of early snow release, e.g. C. tetragona in most microsites, had a quiescent period of slow growth (<5-10% of season's total) prior to the onset of rapid growth. This pattern was similar to, but asynchronous with reproductive development. Growth was only roughly correlated with snow release. Seasonal growth patterns were advanced in 1975 when melt out occurred approximately two weeks earlier than in 1974, and growth periods were delayed both years in plants of late snow release. However, the period of most growth was not advanced in plants of early snow release, suggesting an environmental control unrelated to snow cover.

Air temperatures and radiation levels were only partially limiting to growth of C. tetragona during the quiescent period in early snow released microsites. While air temperatures and radiation levels were generally lower during June than during the period of most growth in July and August, growth did occur during certain periods in August when air temperatures and radiation levels were similar to those during the quiescent period. Plant canopy microenvironments certainly influenced the early season's growth but did not directly control the timing of the period of most growth.

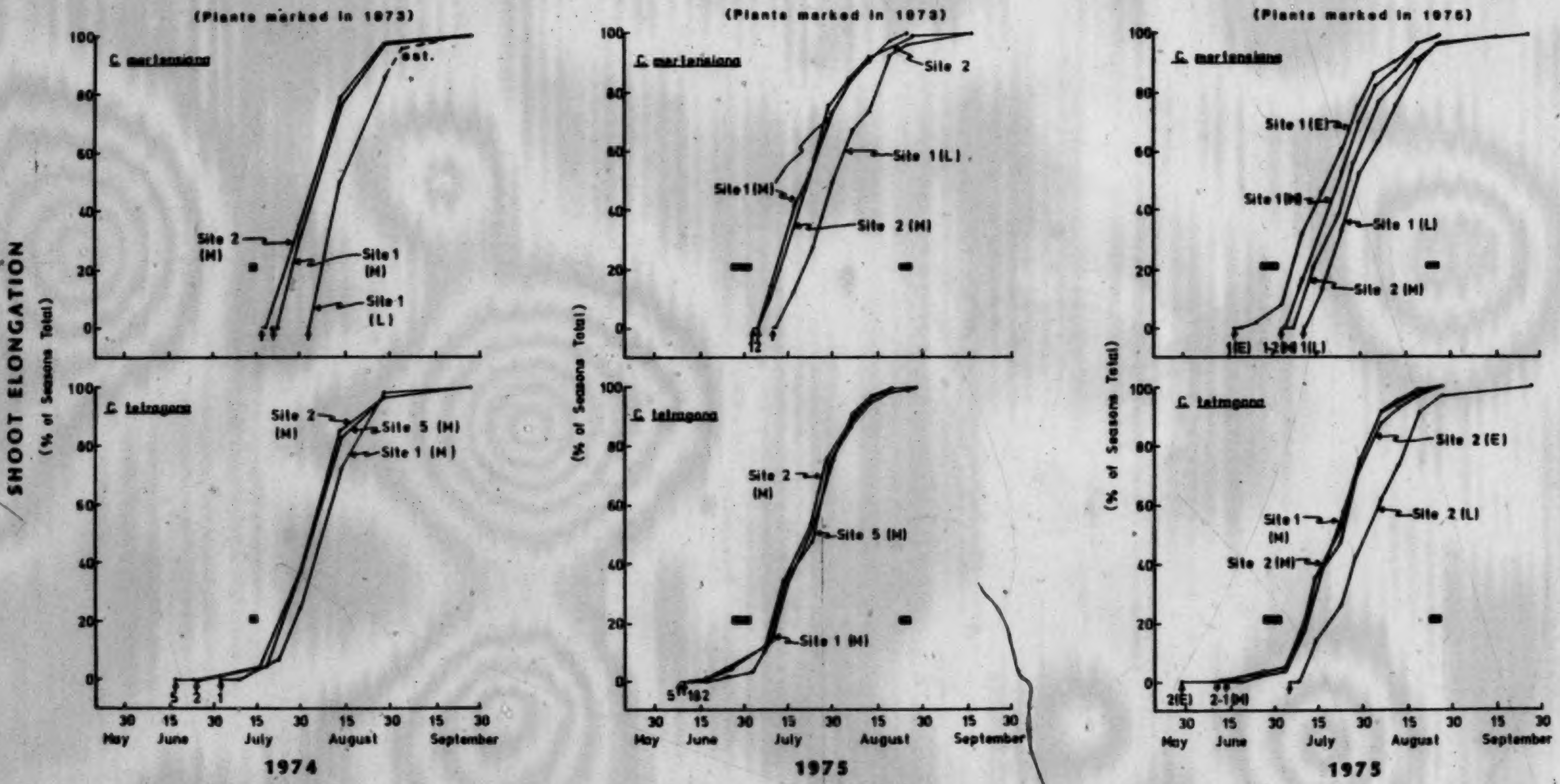


Figure 30. Shoot elongation (as % of seasons total) of Cassiope at various microsites in 1974 and 1975. Included are plants marked in 1973, and additional plants marked along a snow release gradient in 1975 (see Table 13). Indicated are snow release dates (arrows), snow release relative to other microsites at Site (E = early; M = mid; L = late), and summer snow cover (bars).

Table 14. Summary of 1974 and 1975 shoot elongation (growth) data of Cassiope at various microsites. Indicated are snow release relative to other microsites at Site (E=early; M=mid; L=late), number of measured shoots (n), and CI.95.

	C. mertensiana				C. tetragona				
	Site 1 (E)	Site 1 (M)	Site 1 (L)	Site 2 (M)	Site 1 (M)	Site 2 (E)	Site 2 (M)	Site 2 (L)	Site 5 (M)
1974 (Plants marked in 1973)									
		n=19	n=12	n=57	n=67		n=63		n=57
Snow Release (Day 0)		21 Jul	2 Aug	16 Jul	3 Jul		24 Jun		15 Jun
Start of Rapid Growth (Day)		22 Jul (+1)	2 Aug (0)	18 Jul (+2)	23 Jul (+20)		17 Jul (+23)		18 Jul (+33)
>50% Growth (Day)		5 Aug (+15)	13 Aug (+11)	4 Aug (+19)	7 Aug (+35)		3 Aug (+40)		3 Aug (+49)
>95% Growth (Day)		27 Aug (+37)	3 Sep (+32)	27 Aug (+42)	26 Aug (+54)		26 Aug (+63)		26 Aug (+72)
Total Growth (mm)		4.1 ±0.8	2.6 ±0.6	3.8 ±0.4	5.3 ±0.4		4.3 ±0.5		4.9 ±0.5
Max. Rate (mm/d)		0.17±0.05	0.14±0.03	0.12±0.01	0.18±0.02		0.16±0.02		0.17±0.02
1975 (Plants marked in 1973)									
		n=19	n=12	n=57	n=67		n=63		n=57
Snow Release (Day 0)		3 Jul	10 Jul	4 Jul	9 Jun		9 Jun		8 Jun
Start of Rapid Growth (Day)		4 Jul (+1)	11 Jul (+1)	4 Jul (+0)	5 Jul (+26)		7 Jul (+28)		7 Jul (+27)
>50% Growth (Day)		21 Jul (+18)	30 Jul (+20)	22 Jul (+18)	22 Jul (+43)		21 Jul (+42)		24 Jul (+44)
>95% Growth (Day)		17 Aug (+45)	23 Aug (+44)	19 Aug (+46)	10 Aug (+62)		11 Aug (+63)		12 Aug (+62)
Total Growth (mm)		7.3 ±1.1	5.7 ±1.0	5.8 ±0.6	5.6 ±0.4		4.5 ±0.6		5.1 ±0.6
Max. Rate (mm/d)		0.25±0.05	0.20±0.03	0.21±0.02	0.20±0.02		0.20±0.04		0.23±0.03

Table 14. (continued)

	C. mertensiana				*C. tetragona*				
	Site 1 (E)	Site 1 (M)	Site 1 (L)	Site 2 (M)	Site 1 (M)	Site 2 (E)	Site 2 (M)	Site 2 (L)	Site 5 (M)
	1975 (Plants marked in 1975)								
	n=21	n=21	n=22	n=19	n=25	n=22	n=25	n=25	
Snow Release (Day 0)	17 Jun	3 Jul	10 Jul	3 Jul	13 Jun	29 May	10 Jun	4 Jul	
Start of Rapid Growth (Day)	4 Jul (+17)	4 Jul (+1)	12 Jul (+2)	7 Jul (+4)	4 Jul (+21)	4 Jul (+36)	4 Jul (+24)	8 Jul (+4)	
>50% Growth (Day)	19 Jul (+32)	21 Jul (+18)	30 Jul (+20)	27 Jul (+24)	21 Jul (+38)	24 Jul (+56)	22 Jul (+42)	1 Aug (+28)	
>95% Growth (Day)	17 Aug (+61)	19 Aug (+45)	25 Aug (+46)	25 Aug (+52)	14 Aug (+62)	16 Aug (+79)	11 Aug (+62)	24 Aug (+51)	
Total Growth(mm)	5.4 ±0.8	8.2 ±1.0	6.9 ±0.7	5.2 ±0.9	5.8 ±0.8	7.4 ±0.8	5.8 ±0.6	6.7 ±0.9	
Max. Rate (mm/d)	0.17±0.02	0.24±0.04	0.22±0.04	0.18±0.04	0.17±0.02	0.32±0.06	0.22±0.04	0.23±0.04	

The onset of the period of most growth coincided with rapidly rising soil temperatures in the rooting zone (see Microclimate Section). Soil temperatures at -10 cm in 1975 were *ca*. 0°C in *C*. *mertensiana* microsites and *ca*. 1.0°C in *C*. *tetragona* microsites during the week preceding the start of rapid growth. Soil temperatures were 0.5-1.5°C and 2-5°C in the respective microsites at the onset of rapid growth, and rose rapidly thereafter. The primary factors retarding the rise of soil temperatures were the percolation of meltwaters in *C*. *tetragona* microsites and snow cover in *C*. *mertensiana* microsites.

Most shoot elongation (90-95% of season's total) occurred over a period of 5-7 wk in July and August of both years and coincided with the period of maximum seasonal soil temperatures, air temperatures, and radiation. The duration of the rapid growth period of *C*. *mertensiana* in 1975 was approximately one week longer than in 1974. Growth completion was probably delayed by the cool, rainy conditions during August, 1975. Growth was essentially complete by September of both years at all microsites. A small amount of growth (<5% of season's total) was measured at some microsites during September. This may simply be an artifact of the reduced sampling frequency during this period, but more likely represents hydration of the following year's leaves rather than any elongation of current year's stem segments.

Species differences in total seasonal shoot growth were not pronounced but trends are suggested (Table 14). Seasonal growth of both species averaged 5.5 mm/yr ($\bar{X}$ of all microsites in both years) but was more variable in C. mertensiana (2.6-8.2 mm/yr) than C. tetragona (4.3-7.4 mm/yr). Growth of both species was reduced in 1974 compared with 1975, but only significantly in C. mertensiana. This suggests that a shortened growing season following a winter of heavy snowfall and late snow release is more detrimental to shoot growth of C. mertensiana. Growth of C. mertensiana was greatest at the Site 1 mid snow release microsite, and was reduced, in most cases significantly, in exposed, late snow release, or high elevation microsites. Shoot growth of C. tetragona presented some anomalous trends, not clearly related to microsites. Growth was significantly less at the Site 2 mid snow release microsite than at the Site 1 mid snow release microsite, but was greatest at the Site 2 early snow release microsite. Growth of C. tetragona was more consistent and less influenced by microsite conditions than C. mertensiana.

The maximum rates of shoot growth, calculated over the approximate weekly measurement intervals, were low in both species (ca. 0.20 mm/d). Species differences in contrasting years and microsites followed the same patterns as total shoot growth, although few were significant.

Shoot Chronologies

No statistical differences were found in the yearly growth increments and leaf production of basal shoots of *C. tetragona* from early, mid, and late snow release microsites at Site 2 (Table 15). Seven consecutive year's growth intervals were identifiable (variable between shoots) by old leaves and pedicels. Growth increments averaged *ca*. 9 mm/yr, and ranged between 4-15 mm/yr. Shoot growth was highly variable; two shoots often showed contrasting patterns of high and low growth in consecutive years. Yearly leaf production averaged *ca*. 9 pairs of leaves per year, and ranged between 4-23 pairs per year. Leaf production followed the same pattern of variability as shoot growth. Only the basal canopy shoots consistently flower each year allowing chronological sequencing, and this suggests that these shoots may experience less variable conditions than the "average" canopy shoots as marked for measurements of shoot elongation. This may partially explain the lack of differences between years or microsites as well as the greater shoot elongations compared to the marked shoots. Also, environmental conditions over three consecutive years (year 1 = primorida differentiation; year 2 = partial stem elongation and leaf expansion; year 3 = completion of stem elongation and leaf expansion) influence final stem growth and leaf production, and this may tend to suppress yearly and microsite differences.

Table 15. Chronology of seasonal shoot growth, leaf and flower production, and numbers of years of fully expanded living leaves in C. *tetragona* along a snow release gradient at Site 2. Sample size (n), range, and CI.95 are indicated.

Snow Release	1974	1973	1972	1971	1970	1969	1968
			Growth per year (mm)				
Early	10.1±3.1 (6-15) n=25	9.4±1.0 (6-15) n=25	8.4±0.8 (6-15) n=25	8.3±1.0 (4-13) n=23	8.8±0.8 (6-12) n=17	8.0±1.0 (6-11) n=10	9.3±1.8 (7-14) n=8
Mid	7.8±0.8 (4-13) n=31	9.1±0.7 (4-13) n=30	8.8±0.9 (4-14) n=30	8.2±0.8 (4-14) n=29	8.8±0.7 (6-12) n=26	8.7±0.9 (5-13) n=19	10.6±2.2 (8-15) n=8
Late	7.2±0.5 (5-10) n=30	9.4±0.9 (5-15) n=30	8.8±1.0 (4-15) n=30	9.4±1.0 (6-15) n=26	9.5±1.1 (5-14) n=19	7.8±2.7 (5-10) n=5	9 -- n=1
			Pairs of leaves per year				
Early	9.2±0.6 (7-13)	10.0±0.6 (8-13)	9.2±0.6 (7-13)	9.1±0.7 (6-12)	8.8±0.6 (7-10)	7.8±0.7 (6-9)	8.5±1.0 (7-11)
Mid	8.5±0.9 (4-14)	10.2±1.1 (7-23)	8.6±1.6 (6-18)	9.1±0.6 (6-13)	9.7±0.7 (8-16)	8.9±0.8 (6-12)	9.6±1.4 (8-12)
Late	7.7±0.8 (4-12)	9.3±1.0 (6-20)	9.0±0.9 (6-15)	9.0±0.6 (7-12)	9.6±0.6 (6-12)	8.0±1.5 (6-9)	8 --
			Flowers per year				
Early	4.2±0.6 (2-6)	3.2±0.5 (0-5)	3.0±0.4 (0-4)	3.6±0.5 (2-6)	2.9±0.5 (1-4)	3.4±0.8 (1-4)	2.6±0.8 (2-4)
Mid	3.4±0.4 (2-6)	2.4±0.4 (0-4)	2.3±0.4 (0-4)	2.4±0.3 (1-4)	2.3±0.4 (1-4)	2.3±0.4 (0-4)	3.0±0.6 (2-4)
Late	3.0±0.3 (2-4)	1.8±0.3 (0-3)	2.1±0.4 (0-4)	2.7±0.4 (1-5)	2.2±0.3 (1-3)	1.6±1.4 (0-3)	2 --
			Years of living leaves				
Early	2.4±0.3		Mid	2.0±0.5	Late	3.1±0.2	

Differences in yearly flower production were often significant but not clearly related to patterns of shoot growth or leaf production during either the current or the previous year. This agrees with the observation noted with the plants marked for phenological observations and growth measurements that reproductive development is influenced by different environmental factors than shoot elongation. Microsite differences in flower production were more pronounced. The mean yearly flower production over the seven years of record was 3.3 ± 0.5, 2.6 ± 0.4, and 2.2 ± 0.5 flowers per year (± CI.95) in early, mid, and late snow release microsites, respectively. This suggests that early snow release is conducive to greater flower production in _C. tetragona_. Similar trends were noted with the upper canopy shoots of the plants marked for phenological observations. The frequency of shoot flowering and flower production were recorded on the marked plants in 1973 (Table 16) and _C. tetragona_ had greater flower production at the higher elevation, more exposed Site 5. _Cassiope mertensiana_ followed a similar pattern of reduced flowering in the late snow release microsite. However, in contrast to _C. tetragona_, flowering in _C. mertensiana_ was also reduced at the higher elevation microsite.

Leaf longevity of _C. tetragona_ was significantly greater in the late snow release microsite (Table 15). The number of years of fully expanded living leaves in fall collected shoots ranged between one and four, and averaged

Table 16. Frequency of shoot flowering and flower production in 1973 on plants marked for phenological observations. Indicated are snow release relative to other microsites at Site (M=Mid; L=Late).

	C. mertensiana			*C. tetragona*		
	Site 1 (M)	Site 1 (L)	Site 2 (M)	Site 1 (M)	Site 2 (M)	Site 5 (M)
Flowering Frequency	50%	6%	38%	53%	30%	66%
Flowers Per Flowering Shoot	2.1	1.3	1.7	1.9	1.9	2.2

2.0-2.4 in the early and mid snow release microsites, and 3.1 in the late snow release microsite. Values would be one year greater if measured in mid summer, before senescence of older leaves. Reduced leaf longevity in exposed microsites may be a function of more rigorous environmental conditions. However, greater leaf longevity in late snow release microsites may represent a physiological adaptation to maximize photosynthesis and storage of nutrients and food reserves in areas with a reduced growth period. Observations were also made on leaf longevity of *C. mertensiana*, and similar trends were noted. Mature leaves remained living for *ca*. 5-7 yr in mid snow release microsites, but leaf longevity often exceeded 10 yr in protected microsites. The greater leaf longevity of *C. mertensiana* may give it a competitive advantage over *C. tetragona* in microsites of late snow release.

Observations of Reproductive Strategies

The visual floral displays of treeline vegetation, especially heath species, are impressive. Cassiope flowers vigorously in most habitats, often producing six or more flowers per flowering shoot. This must represent a significant energy expenditure on sexual reproduction, considering the slow growth rates. However, sexual reproduction appears to play only a minor role at the present time in the maintenance of local populations, as discussed below.

Seed production by Cassiope is high, except where limited by reduced flowering and incomplete fruit maturation in areas of late snow release (primarily C. mertensiana). The small seeds, ca. 0.7 X 0.15 mm, are readily wind dispersed into most habitats. Capsule dehiscence of C. tetragona often occurs during winter when terminal portions of shoots and erect capsules project above the snow pack, allowing seeds to be dispersed considerable distances. This manner of winter seed dispersal is common in arctic plants (Savile 1972). High seed production may not be accompanied by high seed viability or germination rates.

Germination tests were conducted with seeds of both species collected from mid snow release microsites at Sites 1 and 2 on 3 September, 1973, and 29-30 October, 1974. Seeds had been stratified by temperatures <0°C in the field before collection, and were stored dry at 5°C for ca. one month before tests. Germination tests were conducted on moist filter paper in petri dishes at 20°C (light and dark), and terminated after 21 days. No germination was observed for either C. mertensiana or C. tetragona, suggesting incomplete ripening or stratification, improper conditions for germination, or low seed viability.

Successful seedling establishment appears to occur infrequently as no seedlings were observed in any habitats during the course of this study. This may be due to a lack of seedling recognition because of their small size, or to an actual absence of seedlings. Reproduction by seeds must have occurred in the past. However, only in limited areas are plants recognizable that probably established from seeds. Both species were observed colonizing Neoglacial moraines in Jasper National Park. Also, small plants of both species were observed on Signal Mountain in areas of late snow release with reduced vascular plant cover. The smallest and presumably youngest plants observed were estimated at ca. 15+ years old. Precise ageing using shoot chronologies is impossible on these plants due to slow growth rates, the maintenance of a seedling size for several years, and the lack of flowering. Seedling establishment is probably inhibited in exposed microsites due to rigorous microenvironments. The vigorous growth of vascular and moss species, and needle ice activity in bare areas, probably inhibits seedling establishment in C. mertensiana and C. tetragona communities.

Both species of Cassiope reproduce aggressively in their normal habitats by vegetative means. Rhizomes permeate the LFH and Ah soil horizons and decumbent shoots readily produce adventituous roots. Individual plants of C. mertensiana are normally impossible to separate, either above or below ground. The scattered or relatively open spacing of C. tetragona is also more an apparent rather than a real plant separation. The more distinct clumps of both species appear to be approximately of the same age, ca. 30-50 years or more old, and may represent vegetative reproduction of plants established from seed at a much earlier date. Observations in other areas of the Canadian Cordilleras on the uniformity of plant size (and perhaps age), and patterns of flavonoid chemistry of local populations of C. mertensiana and C. tetragona, suggest that they may represent essentially clones with a long history of vegetative reproduction from an older period of plant establishment (Denford and Karas 1975, and Denford pers. comm.). Vegetative reproduction appears to be responsible for the maintenance of local populations of Cassiope at the present time. Sexual reproduction was observed to operate only to extend plants into new habitats or at the limits of the species tolerances.

B. Cold Hardiness

a. Methods

Cassiope mertensiana and Cassiope tetragona plants used in controlled environment studies, including cold hardiness tests, were collected from late snow release microsites near Site 1 and exposed microsites near Site 2, respectively. Collection site soils were retained as the potting medium. Plants were maintained in the laboratory and cycled through summer, fall, and winter regimes to synchronize desired phenological and hardiness states. Other potted plants remained on Signal Mountain in their respective communities in an excavation in the soil to maintain normal plant canopy heights. Thus, these plants were subjected to near normal Cassiope microenvironments and cold acclimation before removal to the laboratory.

Summer conditions were simulated in the laboratory by growing plants in a Trop-Arctic greenhouse under natural daylength extended to a 16 h photoperiod with multivapour and Lucalox lamps giving an irradiance of >250 $\mu E \bullet m^{-2} \bullet s^{-1}$ PhAR (photosynthetically active radiation) at the canopy level. Air temperatures were regulated such that the maximum of 15-17°C occurred at 1200-1400 h and the minimum of 7.5-10°C occurred near 2400 h. Relative humidity was controlled in steps with a low of 35-50% from 1000-1700 h, and a high of 95-100% from 0300-1000 h. Plants were watered daily with tap water. After completion of the growth cycle plants were transferred to controlled environment chambers

(Environmental Growth Chambers, Chagrin Falls, Ohio) for hardening. Fall conditions were simulated by an 8 h photoperiod with fluorescent and incandescent lamps. The irradiance was stepped up and down in two steps to give a maximum irradiance of *ca*. $250\,\mu E\bullet m^{-2}\bullet s^{-1}$ PhAR at the canopy level. Temperatures during the light and dark periods were +5°C and -2°C, respectively. Humidity was not controlled and fluctuated between *ca*. 50% and 80%. After four to six weeks, dormant, hardened plants were covered with plastic bags (often with crushed ice or snow), and transferred to a dark cold room at -2°C to -4°C to simulate winter conditions. After a minimum of six weeks, plants were transferred to the Trop-Arctic greenhouse and summer conditions.

Cold hardiness tests were conducted on plants of three hardiness states: summer plants in full flower, partially hardened fall plants, and fully hardened winter plants. Tests were conducted with plants taken from the controlled environment conditions described above, and with plants collected from Signal Mountain in the fall and early winter. Partially hardened fall plants were collected from the field in early October, 1975, and kept for one month under fall conditions as described above until tests began. These plants had been exposed to temperatures *ca*. -5°C before removal from Signal. Hardened winter plants were collected from the field in early November, 1975, and stored for one week under winter conditions as described above until tested. These plants had been exposed to temperatures *ca*.

-10°C (C. mertensiana before snow cover) and ca. -15°C (C. tetragona) before removal from Signal.

Tests were conducted using either whole plants or cut shoots because of plant number and space limitations. Shoots were cut under water and placed in moist sand. The shoots could be maintained for the test duration without injury. Potted plants and sand cultures with two vigorous shoots of each species and three hardiness states were placed in a freezing cabinet at -2°C to equilibrate for two hours. Cabinet temperature was gradually lowered at 1.5°C per hour to -40°C. Test plants were removed after exposure to desired temperatures and either rewarmed or stored for two months in dark cold chambers at -25°C and -40°C. Air and leaf temperatures during freezing tests were measured with 0.127 mm thermocouples and recorded on a Data Aquisition System (Easterline Angus Model D2020). Plants were transferred from cold temperatures in a precooled insulated chest to a dark cold room at -2°C to -4°C for a four-hour equilibration. Plants were then placed in a dark cool room at +4.5°C for one week, and subsequently transferred to a Trop-Arctic greenhouse and summer conditions. Freezing damage was visually rated (Table 17) after six weeks in summer conditions. Freezing injury resulted in partial to complete browning of leaves and buds and was easy to assess. No difference was observed in the freezing injury of whole plants or cut shoots. Viable plants or shoots frequently flowered after freezing tests.

Table 17. The effect of low temperature on Cassiope leaf tissue viability. Summer plants were taken from the laboratory and fall and winter plants from Signal Mountain.

	TREATMENT TEMPERATURE					
	-2°C	-5°C	-10°C	-16°C	-26°C	-36°C
			1 hour at temperature			
C. mertensiana						
Summer	0	0	1	4	4	4
Fall	0	0	0	0	1	2
Winter	0	0	0	0	2	3
C. tetragona						
Summer	0	0	0	4	4	4
Fall	0	0	0	0	0	1
Winter	0	0	0	0	0	0
			2 months at temperature			
					-25°C	-40°C
C. mertensiana						
Summer					4	4
Fall					3	4
Winter					4	4
C. tetragona						
Summer					4	4
Fall					1	2
Winter					3	4

0 = No injury, similar to control.
1 = Slight injury, browning of apical leaves or leaf discoloration.
2 = Moderate injury, ca. 50% of leaves brown.
3 = Severe injury, all leaves brown except protected buds and apices.
4 = Tissue completely dead!

b. Results

Summer flowering plants of both species were able to tolerate -10°C with little or no visual injury, but both were killed at -16°C (Table 17 and Figure 31). The survival temperature was below the minimum temperatures encountered in Cassiope habitats during the study, May through September. Fall and winter-hardened plants of C. mertensiana were injured after one hour exposure to -26°C, and severely injured at -36°C. Cassiope tetragona was able to tolerate one hour exposure to -36°C with little or no injury. Thus, a differential sensitivity exists to temperatures that normally occur in very exposed Cassiope habitats during winter.

Two months exposure to low temperatures resulted in greater tissue damage in both species (Table 17 and Fig. 31). Fall and winter-hardened plants of C. mertensiana were severely injured or killed at -25°C, and all plants were killed at -40°C. Cassiope tetragona was slightly to severely injured at -25°C, but some plants were able to tolerate -40°C. Temperatures this low do not normally occur for this duration in Cassiope habitats during winter.

The cold hardiness of plants acclimated in the laboratory under fall conditions was similar to those stored under winter conditions of continuous darkness and subfreezing temperatures. Also, plants collected from Signal in November did not possess greater cold hardiness than those collected in October. Weiser (1970) suggests that near

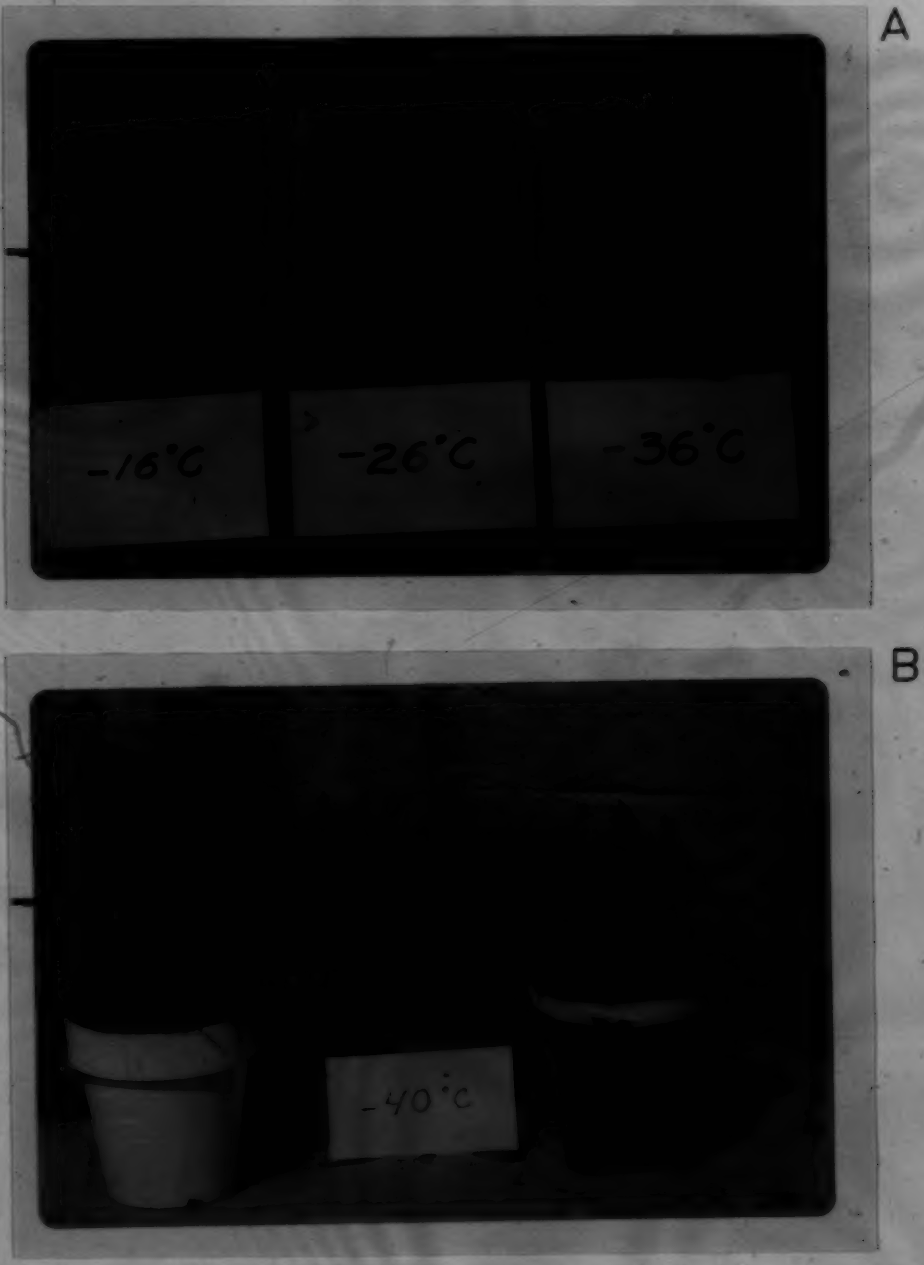


Figure 31. Low temperature injury to C. mertensiana and C. tetragona.

a. Cut shoots in sand exposed to one hour at designated temperature. Included are summer shoots (left column), partially hardened fall shoots (middle column), and hardened winter shoots (right column) of C. mertensiana (top two rows) and C. tetragona (bottom two rows).

b. Hardened winter plants (C. mertensiana on left) exposed to -40°C for two months.

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Images en couleur

maximum hardiness occurs during the second stage of acclimation, after induction by short day photoperiods and low temperatures. The results with fall and winter-hardened Cassiope, both laboratory and field acclimated, agree with this model. The near maximum hardiness of Cassiope is probably reached in September or October, prior to the intense cold periods of winter.

The cold hardiness of plants in the laboratory under fall and winter conditions was similar to plants taken from Signal in early October. However, the field plants were stored for one month under the same fall conditions as laboratory plants, and acclimation would be similar. The plants collected from Signal in October were more hardy than those collected in November. This anomalous difference was more pronounced in the two month low temperature treatment. Leaves that survived two months at -25°C and -40°C were visibly rugose, indicating intense dehydration. The increased survival of fall-hardened plants may not be due to greater cold hardiness, but rather to greater initial leaf hydration and a shorter period of exposure to severe dehydration. Fall-hardened plants were watered daily in the laboratory, whereas field plants collected in November had been exposed to some fall and early winter desiccation and were not watered prior to freezing tests. Low temperature-induced dehydration may be important in limiting Cassiope to protected (i.e. snow covered) microsites and in differentiating between the relative exposure tolerances of the species.

C. Water Relations

a. Methods

Water Potentials

Leaf water potential, turgor potential, and osmotic plus matric potential were measured with Spanner-type thermocouple psychrometers (after Mayo 1974) and a psychrometric microvoltmeter (Wescor, Logan, Utah). Sample chambers (*ca*. 8 mm diameter X 4 mm deep) were filled with either leaves or cut sections of leafy shoots, and psychrometers placed in a constant temperature water bath. Water bath temperatures were held at approximately 15°C (field) and 30°C (laboratory); psychrometers were recalibrated and tissue equilibration times determined at the respective temperatures. Psychrometers were equilibrated for 4-6 h and replicate readings taken with the microvoltmeter to ± 0.1 μV repeatability to determine leaf water potential.

Component potentials were determined by freezing the plant tissue and rereading psychrometers. Sample chambers were wrapped in aluminum foil and immersed in either liquid N_2 at -196°C (laboratory) or liquid propane at -42°C (field) for *ca*. 10 min to rupture cell membranes. Chambers were rewarmed for *ca*. 15-30 min and replaced in psychrometers. After 2-4 h equilibration in the water bath, psychrometers were reread to determine osmotic plus matric potential.

Turgor potential was derived as follows:

$$\psi_p = \psi_L - \psi_{\pi+\tau} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (3)$$

where ψ_L = leaf water potential

ψ_p = turgor potential or pressure

$\psi_{\pi+\tau}$ = combined osmotic and matric potential

Leaf temperatures were measured at time of sampling with 0.127 mm thermocouples and a Wescor psychrometric microvoltmeter. Leaf water potentials and component potentials were adjusted to leaf temperatures using the following equation:

$$\psi \text{ at leaf temperature} = \psi \text{ at calibration temperature} \times \frac{T_C}{T_L} \ldots\ldots (4)$$

where T_C = calibration temperature °K

T_L = leaf temperature °K

Water potentials and component potentials were monitored at various microsites at Sites 1 and 2 during June-November, 1975. Composite samples (2-5 replicates per microsite) of current and one year old leaves and included shoot segments were collected from several adjacent plants. Replicate samples usually agreed within ± 0.3 MPa.

Xylem Pressure Potential

Xylem pressure potential (ψ_{xpp}) was measured with a Scholander bomb (PMS Instrument Co., Corvalis, Oregon).

Leafy shoots >5 cm in length were placed in the chamber with <0.5 cm protruding beyond the rubber seal. Bomb pressure was raised rapidly to within 0.5 MPa of the expected value, then slowly at ca. 0.02 MPa per second until water was observed (handlens) to wet the cut surface.

The Scholander bomb was used primarily during the winter months when psychrometry was not possible. Laboratory tests at subzero temperatures indicated that the bomb gave accurate and repeatable measurements of ψ_{xpp} to about -5°C. Below this temperature, liquid water froze the moment it reached the cut surface of the shoot, and the lack of either a color change due to wetting or the bubbling of liquid water caused measurement errors. At subzero temperatures there was also an increase in the frequency of spuriously high readings or readings that were unobtainable at maximum bomb pressure (6.5 MPa). The attainment of high bomb pressures was also limited at low temperatures because of differential contraction of the bomb valves, causing N_2 leakage. To circumvent these problems, samples often were collected, sealed in plastic bags, and transported frozen to a location with favorable measurement conditions. Samples could be read ca. 6 h after collection with virtually no error.

Psychrometry was often conducted in conjunction with Scholander bomb readings. During summer months, ψ_{xpp} was approximately equivalent (±0.3MPa) to ψ_L. During the winter months, ψ_{xpp} was often erroneously low. This was interpretated as due to xylem sap cavitation. During the fall or spring when shoots were immersed in wet snow or meltwater, ψ_{xpp} was often erroneously high. When shoots were saturated with water little pressure was needed to force water from the cut shoots.

Field Estimates of Transpiration

Transpiration in Cassiope was estimated in the field using lysimeters and potometers. The lysimeters weighed 4-5 kg and consisted of plants sealed in a 20 cm diameter X 15 cm deep container using a silicone rubber compound (RTV 30, General Electric) over the soil surface. The potted plants were well watered before sealing, and were replaced with new plants at 2-3 wk intervals. The lysimeters were positioned in a similar sized container buried in the soil to maintain normal canopy height, and were removed periodically and weighed (to ± 0.5g). Lysimeter temperatures (measured with thermocouples) did not differ significantly from the adjacent undisturbed soil. Three lysimeters of each species were used simultaneously and were alternately placed in C. mertensiana and C. tetragona microsites at Sites 1 and 2.

Potometers consisted of shoots (cut underwater) attached via a rubber tube to a fine-scaled pipette (± 0.005 ml). All connections were sealed with five-minute epoxy. Potometers of both species were placed in the plant canopies adjacent to the lysimeters.

Water loss from lysimeters and potometers is expressed on the basis of green tissue dry weights. Senescencing leaves were a minor component and were disregarded.

Vapor Pressure Deficit and Leaf Resistance

The effects of vapor pressure deficit on stomatal response of *Cassiope* were examined using the experimental design of Mayo and Ehret (1980). Cut shoots of hydrated, summer, greenhouse plants (see Cold Hardiness Methods) were sealed in 5 ml vials containing water, and placed in desiccators over saturated salt solutions of known VPD. Dessicators were placed in a controlled environment chamber at 22°C and 70% RH with a 16 h photoperiod; PhAR was 430 $\mu E \bullet m^{-2} \bullet s^{-1}$ at the leaf surface during the light period. Vials plus cut shoots were weighed to determine transpiration on an analytical balance placed inside the chamber.

Relative humidities and VPD's in the desiccators were controlled using saturated salt solutions (Winston and Bates 1960): KCl, 85% RH and 0.35 kPa VPD at 20°C; $Ca(NO_3)_2 \bullet 4H_2O$, 55.5% RH and 1.04 kPa VPD at 20°C; KOH, 8% RH and 2.15 kPa VPD at 20°C. Since KOH was used in one desiccator to control VPD but is known to reduce CO_2 concentrations thus favoring stomatal opening, a few KOH pellets were also placed in the other desiccators. Leaf and desiccator air temperatures were measured with 0.076 mm thermocouples and a Fluke digital thermometer. Relative humidities and VPD's were calculated from actual temperatures. Small fans within desiccators insured air mixing. Wind speed around shoots was 1.3 m/s, measured with a Hastings thermopile anemometer and omni-directional probe.

Leaf resistance (R_L) was calculated according to Slavik (1974):

$$R_L = [(C_{sat} - C_a) / q] - R_a \ldots\ldots\ldots\ldots\ldots (5)$$

where R_L = leaf resistance in s/cm

C_{sat} = saturation absolute humidity at leaf temperature

C_a = absolute humidity at air temperature

q = transpiration rate

R_a = leaf boundary layer resistance

Leaf boundary layer resistance was estimated at ca. 0.1 s/cm due to small leaf size and wind speed around shoots (Nobel 1974).

Leaf areas were determined on the exterior surfaces of intact shoots using the technique of Thompson and Leyton (1971). Leaves of the two species differ in shape and stomata location, and individual shoots differ in the degree of leaf overlap. Thus, the exterior (exposed) leaf surface was chosen here as the most ecologically-meaningful reference area (see "the question of the reference area" in Körner et al. 1979).

Vials plus shoots were placed in desiccators at the start of a dark period. Transpiration of all shoots was determined over two 2-4 h intervals (light and dark) in all desiccators by rotation of vials. Final readings were taken during the second dark and light periods after transfer back to the initial desiccators.

Höfler Diagrams

Höfler-type diagrams were constructed from leaf water potential, component potential, and relative water content data from current leaves of flowering plants and older (1-2 yr) leaves of late summer plants grown in a Trop-Artic greenhouse (see Cold Hardiness Methods). Maximum turgidity was obtained by placing the bases of cut shoots in water in a darkened saturation chamber (100% RH) at 22°C for 2-3 d. Fresh weights increased rapidly during the first day of equilibration and more gradually (1-2% fresh weight per day) thereafter. Turgid shoots were removed from the saturation chamber, partitioned into components (old leaves, new leaves and apices, plus included stem segments), and weighed. Leaves were allowed to air dry in the laboratory to obtain varying tissue hydration levels, and were reweighed and placed in thermocouple psychrometers to determine ψ_L, $\psi_{\pi+\tau}$, and ψ_p. Each determination was a composite of 3-5 shoot segments. Samples were oven dried at 90°C for 24 h and weighed to determine dry weights. Relative water content (R) was calculated after Barrs (1968):

$$R = \frac{\text{fresh weight} - \text{dry weight}}{\text{turgid weight} - \text{dry weight}} \quad \ldots\ldots\ldots\ldots\ldots\ldots (6)$$

The data were analyzed with the model of Acock (1975) to estimate intracellular component potentials, and intra- (symplastic) and extracellular (apoplastic) solution fractions of water in the tissues at various hydration levels. Matrix-bound water content was estimated from the linear regression of R on $1/\psi_{\pi+\tau}$.

An estimate of cell wall elasticity was obtained using the following equation:

$$\mathcal{E} = \frac{\Delta \psi_p}{\Delta R} \quad \text{.........................(7)}$$

where $\mathcal{E}$ = bulk volumetric elastic modulus (Jones and Turner 1978) or bulk modulus (Hellkvist et al. 1974).

Transplants

Plants of C. mertensiana and C. tetragona were transplanted into microsites encompassing the range of normal habitats to compare species survival. Transplants were made in early August, 1974, into: 1) a very exposed Dryas-lichen microsite at Site 2; 2) a mid snow release C. tetragona microsite at Site 2; 3) a mid snow release C. mertensiana microsite at Site 1; and 4) a late snow release Carex nigricans microsite at Site 2. All plants were collected from near Site 2. Six plants of each species were alternately placed in rows at each transplant site with a 1-2 m spacing to minimize disturbance when sampling. Plants were watered frequently until mid September to assure establishment. Various aspects of the water relations of the plants were measured periodically during the winter months (1974-75, and early winter, 1975).

Transplants were sampled for desiccation damage in the summer, 1975. A 25 X 5 cm quadrat frame was placed over each plant, oriented perpendicular to the slope (and prevailing winds) to assure equal sampling of windward shoots showing considerable desiccation and leeward shoots showing little desiccation. Damage was visually rated on a 1-5 scale, the number of shoots counted per category, and the mean heights of shoots in each category recorded. Only shoots >2 cm length were sampled; small lateral branches were disregarded. Shoots were not sampled if they appeared to have been damaged by transplanting. For comparison purposes, plants were also sampled at various locations along the transects at Sites 1 and 2. Ten plants were randomly sampled along a line perpendicular to the transects at each location, except in the very exposed *Dryas*-lichen community at Site 2 where the occurrence of *C. tetragona* was sporadic.

The transplants were also sampled in 1978, four years after transplanting, to determine species survival. Sampling was similar to that for desiccation, and shoot vitality was visually estimated and categorized.

Laboratory Simulation of Winter Desiccation

A laboratory experiment was conducted to simulate winter desiccation of *Cassiope* shoots exposed above the snow. Potted plants were collected from a deep snow accumulation microsite at Site 1 on 20 December, 1974. Plant had not been exposed to prior desiccation due to early winter snow cover. Plants were bagged in plastic and stored outside in Edmonton beneath the snow until early March when they were transferred to a dark cold room at -2 to -4°C for one week. Four potted plants of each species were placed on a permafrost simulator (Younkin 1974) located inside a controlled environment chamber. Soil temperatures were maintained at -2 to -5°C and leaf temperatures at 3 ± 1°C. Chamber, leaf, and soil temperatures were monitored hourly with a Data Aquisition System (Easterline Angus Model D2020) and thermocouples. Chamber relative humidity was maintained at 61 ± 5% (VPD ca. 0.30 kPA). Chamber temperature and VPD approximated the absolute maximum field values recorded during November and April, but were much higher than the mid winter (December-March) maxima (Table 10). An 8 h photoperiod with a combination of fluorescent and incandescent lamps gave ca. 180 $\mu E \bullet m^{-2} \bullet s^{-1}$ PhAR at the canopy level. Fans were situated to blow across the plants and wind speeds were 2.0-2.2 m/s at the front and top of the canopies, and 0.5-0.9 m/s at the rear of the canopies. Leaf tissue samples were collected at midday for water content and psychrometric determinations of Ψ_L, $\Psi_{\pi+\tau}$, and Ψ_p, beginning on day 0 (start of experiment) and periodically over the 10 d experiment duration.

Dehydration Injury of Cut Shoots

Cut shoots of summer and winter Cassiope plants (see Cold Hardiness Methods) were hydrated to R=1.0 (see Höfler Diagrams Methods) and allowed to dehydrate in the laboratory (ca. 20°C and 2.0 kPa VPD) for up to 6-12 h. Shoots were weighed to determine dehydration levels, were replaced in humid chambers as for initial saturation to full turgidity and reweighed to determine rehydration levels, and were oven-dried at 90°C for 24 h and weighed to determine dry weights. Observable injury after rehydration was recorded as minor (slight rugosity and or discoloration) or severe (>50% of leaves rugose, discolored or dead). Weinberger *et al.* (1972), suggests that the failure of tissue to rehydrate to R>0.9 after dehydration can be used as an index of injury. However, *Cassiope* showed no consistent relationship between levels of rehydration and observable injury at high R values. Therefore, observable injury is expressed as a function of hydration level, and rehydration is not reported.

Cavitation in Frozen Stems

Methods similar to those of Hammel (1967) were used to test for the ocurrence of cavitation in the stems of both species following freezing. Experiments were conducted to determine the changes in water uptake of cut shoots and in of intact shoots following freezing of 2 cm stem sections with dry ice (-78.5°C). Liquid N_2 was not used because it could not be easily localized on the small shoots and caused extensive leaf tissue damage.

Shoots were sealed in potometers similar to those used for the field estimates of transpiration. Water loss was initially determined to be equivalent to water uptake by weighing the potometer system and thereafter, only water uptake was recorded. The potometers were equilibrated for 0.5-1 h and readings made at approximately 2 h intervals over a 6 h period prior to freezing. Readings were resumed at *ca*. 1 h post-freezing for a 3 h period. Recovery rates were monitored at *ca*. 14-21 h post-freezing. Rates of water uptake are expressed on the basis of green tissue fresh weights and are 0.48-0.50 of dry weight rates.

The ψ_{xpp} of shoots of intact plants were measured prior to the freezing of experimental shoots. Measurements were taken at 22 h post-freezing of the ψ_{xpp} of experimental shoots that had been frozen and adjacent control shoots that had not been frozen.

Plants used in the cavitation experiments were taken from a Trop-Arctic greenhouse under summer conditions (see Cold Hardiness Methods). Intact plants and potometer systems were maintained for the duration of the experiments in a controlled environment chamber at 20°C and 75% relative humidity, with an irradiance of 280 $\mu E \bullet m^{-2} \bullet s^{-1}$ PhAR at the canopy level.

b. Results

Summer Midday Water Potentials

Both *Cassiope* species followed a similar seasonal course of midday ψ_L and $\psi_{\pi+\tau}$ (Figs. 32 and 33). Leaf water potentials and $\psi_{\pi+\tau}$ were low at snow release and early in the season; *ca*. -2.0 to -3.5 MPa and -2.5 to -5.0 MPa, respectively. This seemed to be environmentally related because a few plants of both species dug from beneath the snow in mid July had ψ_L of *ca*. -1.0 MPa and $\psi_{\pi+\tau}$ of *ca*. -1.5 MPa. However, these plants were from a late snow release

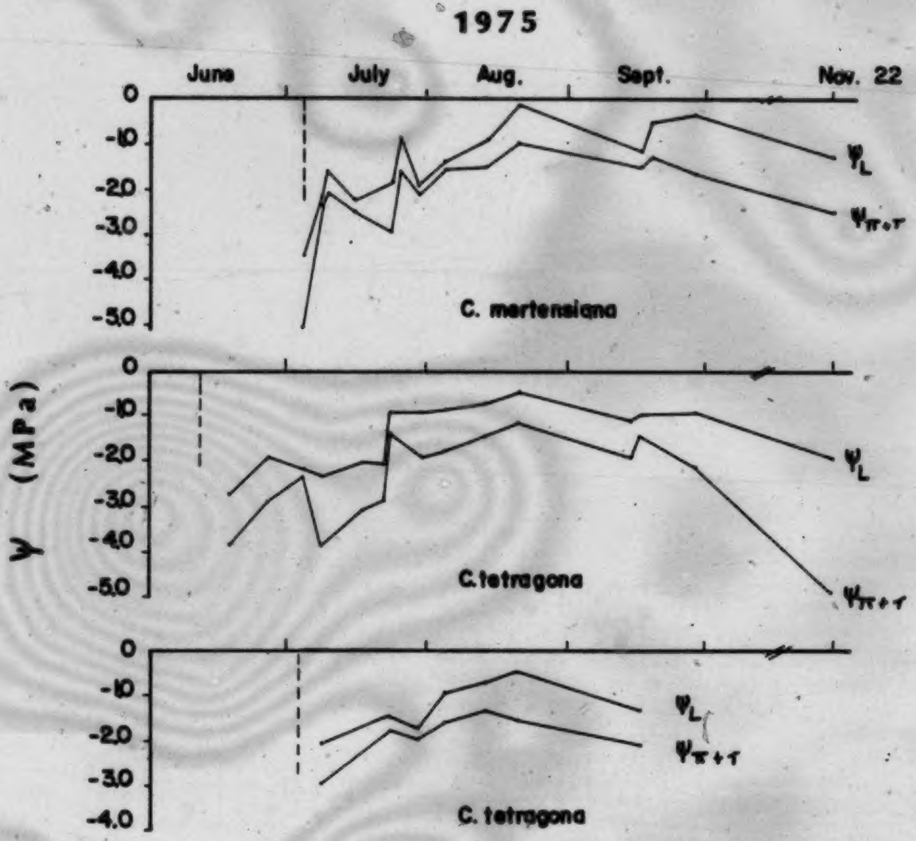


Figure 32. Seasonal course of midday leaf water potentials (Ψ_L) and osmotic plus matric potentials ($\Psi_{\pi+\tau}$) at Site 1 during 1975. Turgor potential is the difference between the two lines. Snow release is indicated by the vertical dashed line. Cassiope tetragona was sampled at two microsites along the snow-release gradient. Data points are means of 2-5 replicates which usually agreed within ± 0.3 MPa (see Methods).

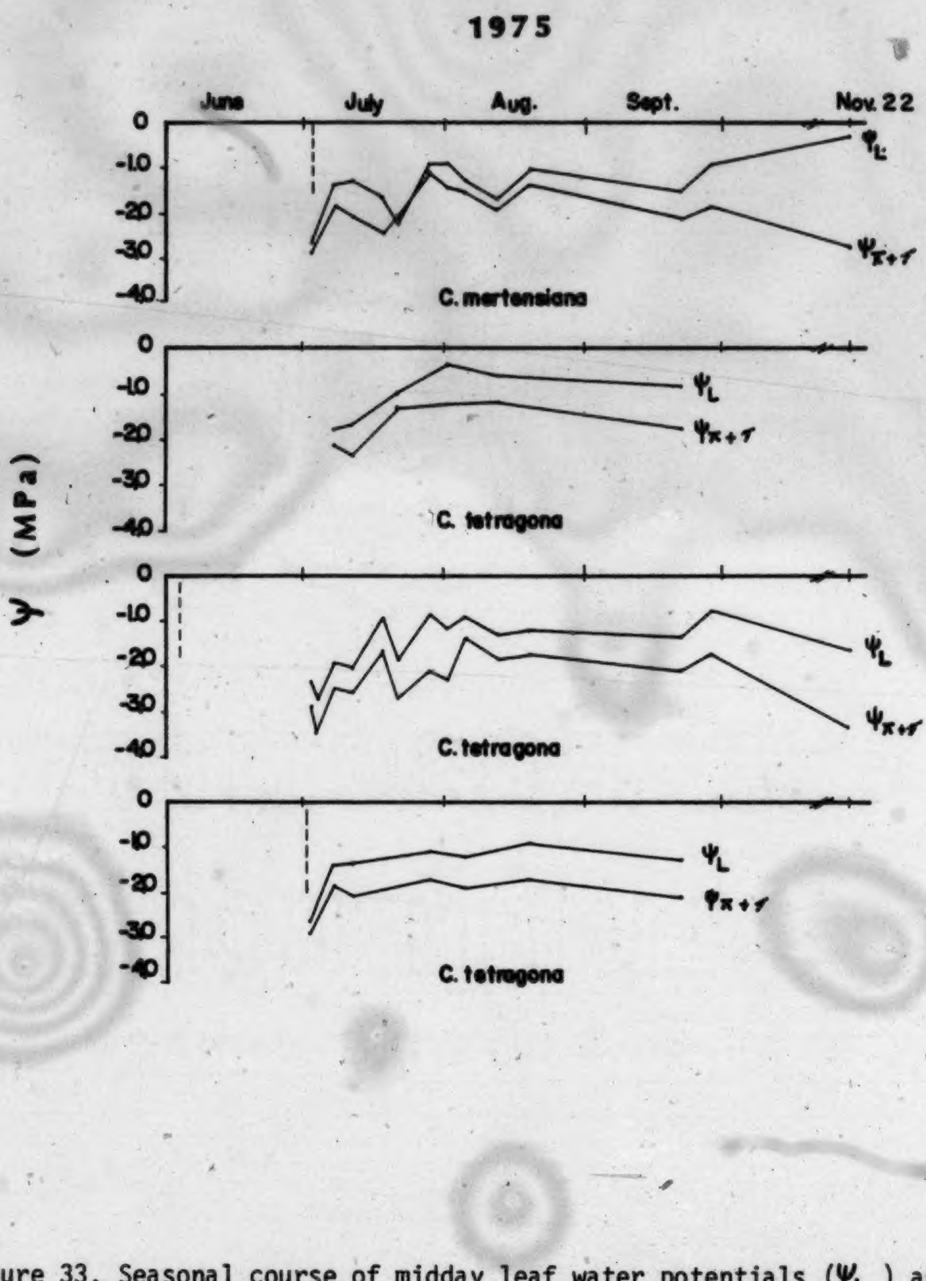


Figure 33. Seasonal course of midday leaf water potentials (Ψ_L) and osmotic plus matric potentials ($\Psi_{\pi+\tau}$) at Site 2 during 1975. Turgor potential is the difference between the two lines. Snow release is indicated by the vertical dashed line. Cassiope tetragona was sampled at three microsites along the snow-release gradient. Data points are means of 2-5 replicates which usually agreed within ± 0.3 MPa (see Methods).

microsite and had experienced early and continuous snow cover through the winter. Leaf and osmotic potentials increased rapidly after snowmelt and the seasonal maxima occurred in mid summer. Maximum ψ_L and $\psi_{\pi+\tau}$ were ca. -0.5 to -1.0 MPa and -1.0 to -1.5 MPa, respectively. Osmotic potentials declined rapidly in October and approached spring levels by late November. Fall ψ_L values paralleled the declining $\psi_{\pi+\tau}$ values except for C. mertensiana at Site 2. This site had experienced the longest period of fall snow cover of any microsite sampled, and ψ_L was at a seasonal high.

Turgor potentials were ca. 0.5 to 1.0 MPa in both species throughout the season. The lowest turgor was measured in July, during a period of high air temperature and VPD. Turgor was relatively constant in C. tetragona but more variable in C. mertensiana. Turgor potentials <0.1 MPa were measured in C. mertensiana at both Sites on several occasions. The minimum ψ_p measured in C. tetragona was 0.26 MPa. Turgor was highest (ca. 2.0 MPa) in late November in snow covered plants, even though ψ_L was below the mid summer maxima.

Low ψ_L values during the spring and in early winter were not indicative of water stress because ψ_p was high in most instances. Periods of slight water stress were indicated in C. mertensiana in mid summer when turgor fell to low levels even though ψ_L remained high. The maintenance of leaf water potentials well below soil water potentials (see Tables 6 and 7) indicates that Cassiope has a high root resistance to water uptake.

Xylem pressure potentials were measured infrequently during the summer months and closely followed ψ_L values. Water contents were also measured infrequently during the summer months. Tissue fresh weights ranged between 220% and 250% of dry weights in both species at all microsites.

Summer Diurnal Water Potentials

Diurnal changes in water potentials were monitored in C. mertensiana and C. tetragona on three and four days, respectively, in July, 1975. Variable microclimatic conditions existed on the sample dates. This allowed species responses to be compared under conditions varying from hot and dry to cool and wet. Contrasting patterns were presented by the species (Fig. 34), Cassiope tetragona maintained relatively constant ψ_p (around 1.0 MPa) regardless of changes in ψ_L or environmental conditions. Cassiope mertensiana did not maintain constant ψ_p and periods of water stress were indicated (e.g. July 9, Site 1).

Leaf water potentials were lowest in C. tetragona on 3 July when air temperatures (to 20°C), radiation (27.9 $MJ \bullet m^{-2} \bullet d^{-1}$), and VPD's (to 1.61 kPa) were high. However, the plants had been covered by snow two days earlier and the soils were saturated with meltwater. Leaf water potential declined during the day to a low of -3.0 MPa in early evening. Turgor potential remained constant even though water was rapidly being lost to the dry atmosphere. Dry

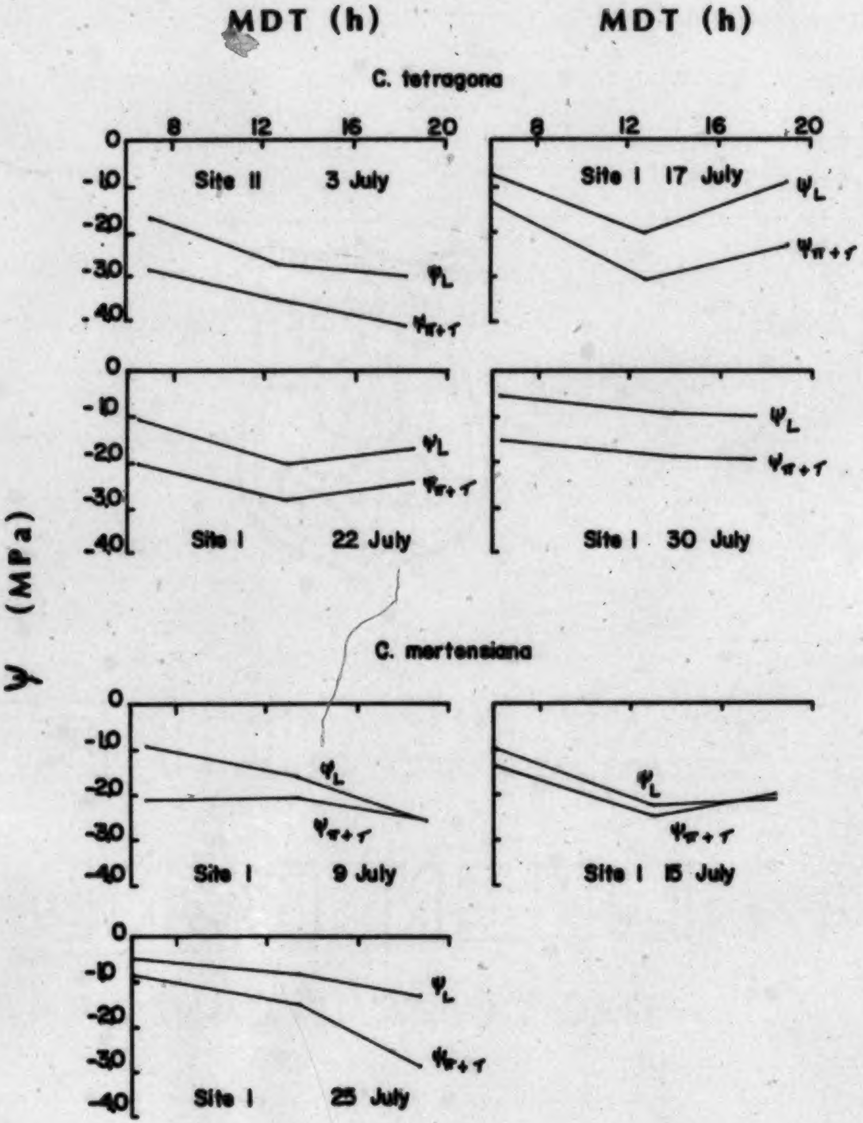


Figure 34. Daily course of leaf water potentials (Ψ_L) and osmotic plus matric potentials ($\Psi_{\pi+\tau}$) during selected days in July, 1975. Turgor potential is the difference between the two lines. Data points are means of 2-5 replicates which usually agreed within ± 0.3 MPa (see Methods).

conditions also existed on 30 July, but were not as extreme. Air temperatures (to 14.5°C), radiation (18.1 $MJ \bullet m^{-2} \bullet d^{-1}$), and VPD's (to 0.95 kPa) were lower than on 3 July, and the magnitude of the change in ψ_L and component potentials was reduced. Conditions were cool, cloudy, with intermittent rain and lower VPD's on 17 July and 22 July, and the midday depression of ψ_L was ameliorated by early evening.

Cassiope mertensiana followed a similar pattern of decreasing ψ_L during the day when exposed to hot, dry conditions (9 July). However, unlike C. tetragona, this was accompanied by a drop in ψ_p. A midday depression of ψ_L and ψ_p also occurred on 15 July. Conditions were cool (to 15.5°C), cloudy (11.7 $MJ \bullet m^{-2} \bullet d^{-1}$), rainy (9 mm ppt. in previous 24 h), and with low VPD's (to 0.33 kPa). High leaf hydration would have been expected. Although precipitation occurred throughout the previous 72 h, plants were exposed to hot, dry conditions for approximately 10 d prior to this and tissue water deficits may not have been alleviated. The anomalously low ψ_p indicates either a low control over water loss or a high resistance to water uptake. Conditions on 25 July were also cool, cloudy, and rainy, but with higher VPD's (to 0.81 kPa). Precipitation was frequent during the preceding days and leaf hydration and ψ_L were high. Leaf water potential dropped only slightly during the day and ψ_p remained high.

Field Estimates of Transpiration

Lysimeters and potometers were maintained during August and early September of 1974 and 1975. Frequent precipitation and ground-level clouds (fog) resulted in saturation of the standing dead of *Cassiope* shoots and invalidated many readings. Reported values are for simultaneous measurements of water loss from lysimeters and potometers taken over 4-10 h midday periods on five dates between 17 August and 3 September, 1974. Plants had reached the end of the growth period and rates of water loss were probably below mid summer levels but higher than in late fall.

Transpiration rates of *C. mertensiana* and *C. tetragona* measured by lysimeters and potometers (*ca*. 0.20-0.25 g $H_2O \bullet g$ dry weight$^{-1} \bullet h^{-1}$) were not significantly different (Table 18). Mean daily rates tended to be slightly higher in *C. mertensiana* than in *C. tetragona*, and maximum daily rates were higher. No significant differences were found due to either Site or microsite placement. Measurement were conducted on days with variable microclimatic conditions. No correlation was found with either mean temperature, mean VPD, total irradiance, or mean wind speed at 15 cm height (top of plant canopy) over the daily measurement periods.

Table 18. Rates of water loss from Cassiope lysimeters and potometers in late summer, 1974. Values are g H_2O•g dry weight green shoots^{-1}•h^{-1}. CI.95 are indicated.

	Mean Daily	Maximum Daily
C. mertensiana		
Lysimeters	0.25 ± 0.06	0.54
Potometers	0.23 ± 0.05	0.48
C. tetragona		
Lysimeters	0.21 ± 0.03	0.34
Potometers	0.20 ± 0.07	0.39

Vapor Pressure Deficit and Leaf Resistance

The stomata of both species showed a normal light-dark response indicating that PhAR was sufficient to cause stomatal opening. Transpiration rates tended to decrease gradually over time, similar to that which occurred in potometers used to study cavitation (Fig. 45). Thus, data reported are for initial light period readings or from shoots with similar initial and final rates.

The effects of VPD on R_L and transpiration are shown in Fig. 35. In both species, R_L increased with increasing VPD. A boundary line fitted after Webb (1972) suggests that increasing VPD causes a greater increase in R in C. mertensiana. Transpiration rates of both species also increased with increasing VPD. This suggests that the increase in R may have resulted from changes in bulk leaf water status rather than a direct effect of VPD upon stomata. Concurrent measurements of ψ_L or relative water

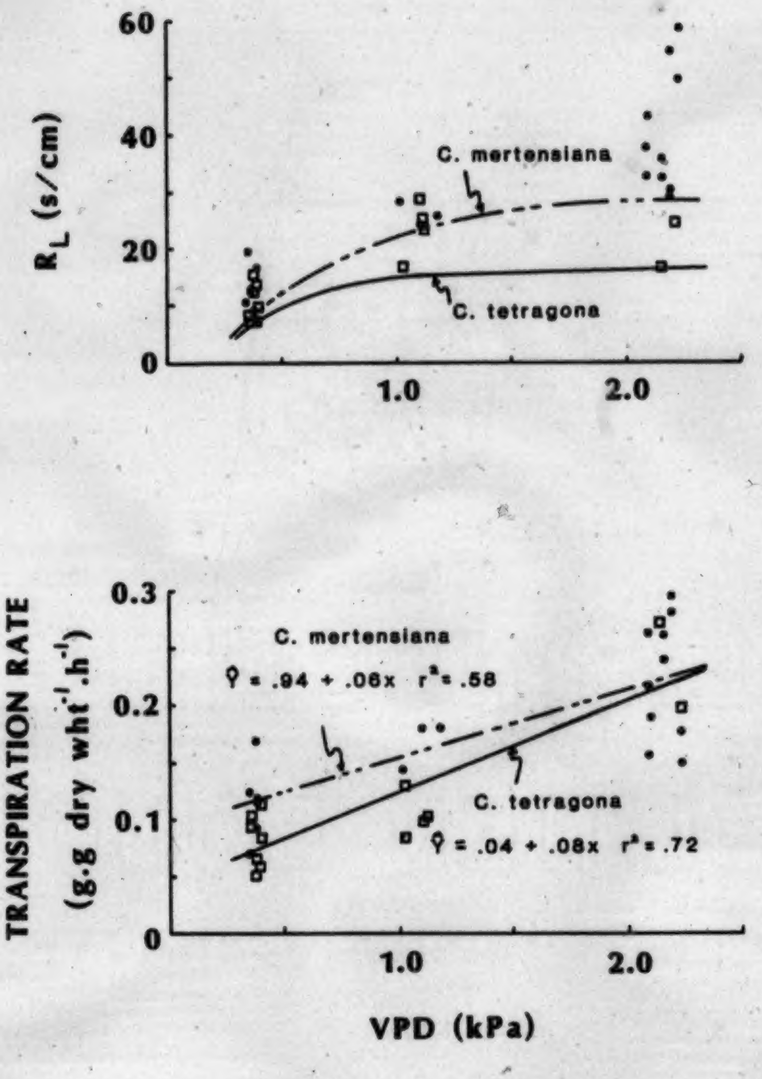


Figure 35. The effects of vapor pressure deficit (VPD) upon transpiration rate and leaf resistance (R_L) of C. mertensiana (○) and C. tetragona (□).

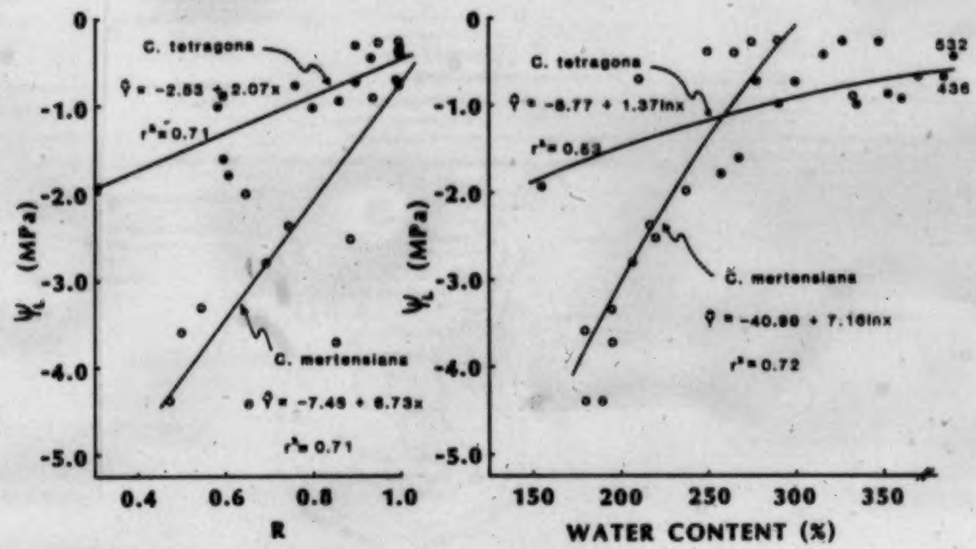
content would have helped to clarify this response.

The minimum leaf resistances measured by this technique were 7-9 cm/s for both species. Subsequent use of a diffusive resistance porometer on intact plants indicated that mimimum leaf resistances are more likely in the range of 1-2 cm/s for both species. The latter are more realistic and agree with values reported for _C_. _mertensiana_ (Edwards 1980) and _C_. _tetragona_ (Oberbauer and Miller 1981) using a null balance diffusion porometer. Thus, the values reported in Fig. 35 should be considered as relative rather than absolute. However, the stomatal closure of _Cassiope_ in response to VPD appears correct and is similar to the response of many species (Johnson and Caldwell 1976, Hall _et al_. 1976, Sheriff 1977).

Höfler Diagrams

The relationship between bulk leaf water potential and tissue hydration of _Cassiope_ grown in the greenhouse under summer conditions is shown in Fig. 36. Old and current leaves of _C_. _mertensiana_ and old leaves of _C_. _tetragona_ showed similar declines in ψ_L with reductions in R. Leaf water potentials at R = 1.0 were _ca_. -0.75 MPa, and declined to -3.75 to -4.25 MPa at R = 0.5. The slope of the line for current leaves of flowering _C_. _tetragona_ shoots was significantly different ($P<0.05$). Leaf water potentials at R = 1.0 were >-0.5 MPa and declined to only _ca_. -1.5 MPa at R = 0.5. Water content at full turgidity also varied with species and leaf age. Mean water contents (fresh weight as

CURRENT LEAVES FLOWERING SHOOTS



OLDER LEAVES LATE SUMMER SHOOTS

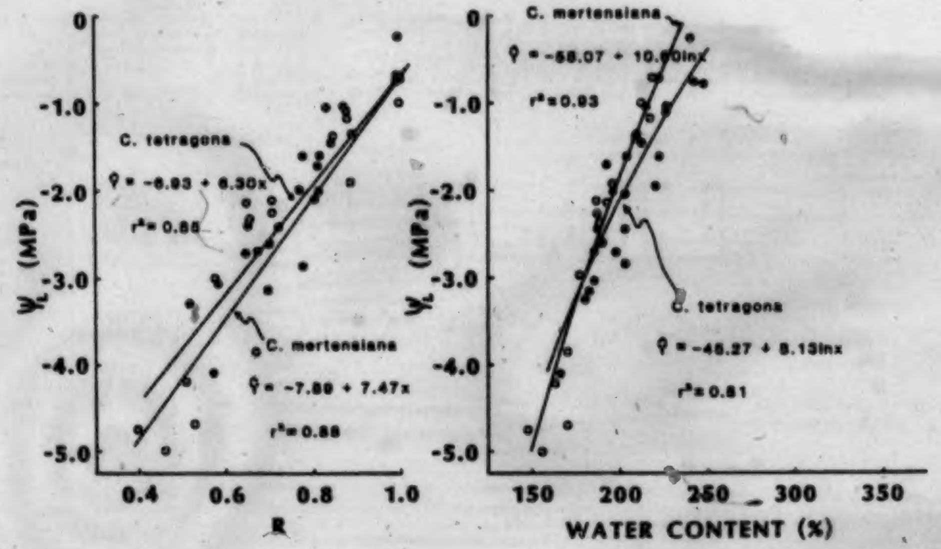


Figure 36. Relationship between bulk leaf water potential, relative water content (R), and water content (fresh weight as per cent of dry weight) of current leaves of flowering shoots and older leaves of late summer shoots of C. mertensiana (○) and C. tetragona (●).

per cent of dry weight ± CI.95) of old and current leaves of *C. mertensiana* and old leaves of *C. tetragona* at R = 1.0 were 226 ± 5%, 265 ± 20%, and 236 ± 6%, respectively. Current leaves of flowering *C. tetragona* shoots had significantly greater water contents at maximum hydration (394 ± 48%).

The extremely high and variable water contents of current leaves of flowering *C. tetragona* shoots at R = 1.0 suggest problems in defining maximum hydration in this tissue. Furthermore, the meaning of full turgor (and thus R) is open to question since ψ_L can never equal zero because $\psi_{\pi+\tau}$ is always negative. Acock (1975) discusses the use of R as a measure of tissue hydration and states it is valid relative to some level of maximum hydration (full turgor) that depends on the measurement method. Boyer (1968) noted that water contents continued to increase after ψ_L had stabilized as leaf tissues were hydrated. Slavik (1974) also suggests that errors may result in R measurements due to the supersaturation of tissues. However, the method used to determine R in the current study was shown by Bannister (1964) to give satisfactory results with other heath species. Therefore, the higher water contents measured at high hydration levels in current leaves of *C. tetragona* compared to the other leaf tissues probably reflect differences in either leaf tissue characteristics or the resistance to water movement between the stem xylem and leaves. It is doubtful that this represents simply an artifact of the technique since all tissues received similar treatment and the hydration of current leaves occurred while attached to shoots.

The slope of the line relating the corresponding reductions in ψ_L to R, i.e. the moisture release curve, has been shown to vary with species, tissue age, and the pretreatment stress history of the plant. However, this relationship is generally regarded as an indication of the drought resistance of the species. Drought-resistant species have steeper slopes, i.e. show a greater reduction in ψ_L with water loss, than drought-intolerant species. Using this criteria, old and current leaves of C. tetragona are more drought resistant than current leaves of C. tetragona. However, both C. mertensiana and C. tetragona are intermediate in drought tolerance when compared to a wide range of taxa (see Maxwell and Redmann 1978).

The Höfler diagrams (Fig. 37) show the partitioning of component potentials with changes in R. The bulk tissue component potentials as measured with thermocouple psychrometers on tissue with ruptured cells do not accurately reflect conditions in the living cells due to the dilution of symplastic water with apoplastic water. Data analyses using the model of Acock (1975) indicate that the apoplastic solution fraction of water in Cassiope is high and intracellular component potentials differ considerably from bulk tissue component potentials. However, the estimates of intracellular component potentials are also

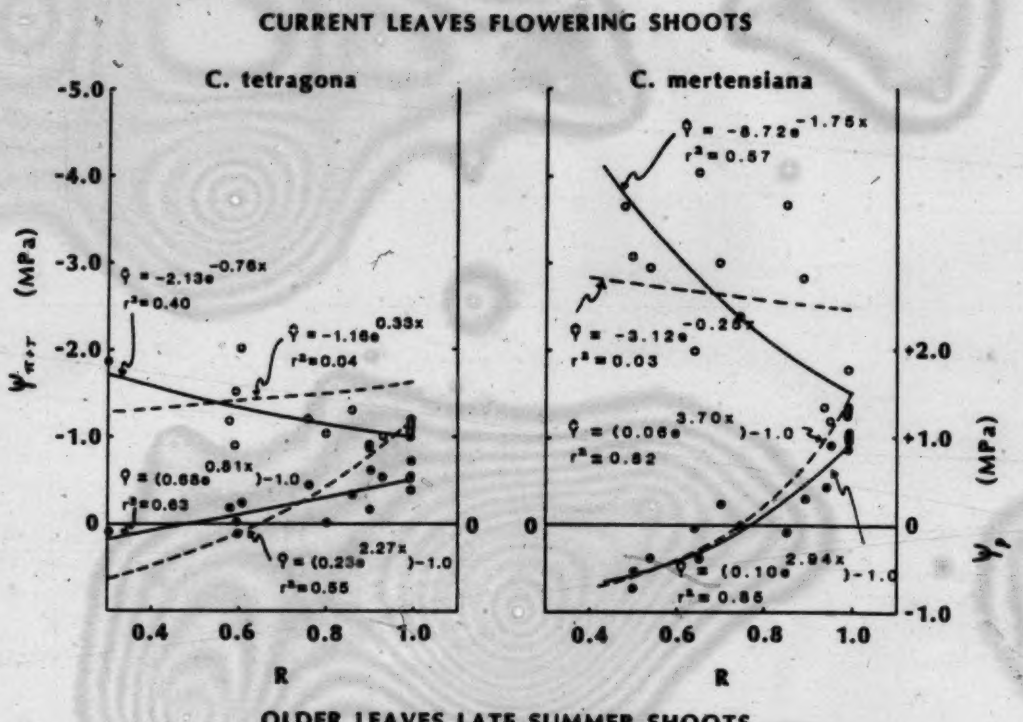


Figure 37. Höfler diagrams showing the relationship between relative water content (R) and the various tissue water potentials of current leaves of flowering shoots and older leaves of late summer shoots of C. mertensiana and C. tetragona. Solid and dashed lines represent bulk tissue potentials and intracellular potentials (after Acock 1975), respectively.

subject to question (note the reversed slope of the regression line of intracellular $\psi_{\pi+\tau}$ for current leaves of C. tetragona). The variability of the original psychrometric data is compounded by errors that accumulate in subsequent model calculations, particularly in the estimates of matrix-bound water content and the apoplastic solution fraction of water at zero turgor. The intracellular component potentials, while physiologically more meaningful, are probably not as reliable for comparison purposes in this instance. Thus, the data will be discussed primarily in terms of the bulk tissue component potentials.

Estimates of maximum $\psi_{\pi+\tau}$ at R = 1.0 obtained from exponential regression lines for current and old leaves of C. tetragona and current and old leaves of C. mertensiana were -1.00, -1.57, -1.51, and -1.26 MPa, respectively. These are comparable with the maximum summer values obtained in the field studies. Estimates of maximum ψ_p at R = 1.0 for the same tissues were 0.52, 0.95, 0.98, and 0.70 MPa, respectively. Actual measured maximum ψ_p obtained at high R were slightly higher, ca. 1.0 MPa for current and old leaves of C. mertensiana and old leaves of C. tetragona, and ca. 0.75 MPa for current leaves of C. tetragona. The latter values are also comparable with the maximum summer values obtained in the field.

Current and old leaves of C. mertensiana and old leaves of C. tetragona showed a relatively rapid decline in $\psi_{\pi+\tau}$ and a concomitant decline in ψ_p with water loss. Regression line estimates of zero turgor were at R values of 0.77, 0.71, and 0.73 in these tissues, respectively. Estimates of $\psi_{\pi+\tau}$ for these respective tissues and R values were -2.26, -2.38 and -2.35 MPa. Current leaves of *C. tetragona* showed a more gradual decline in $\psi_{\pi+\tau}$ and ψ_p with water loss. Zero turgor was reached at R = 0.47 MPa and $\psi_{\pi+\tau} = -1.49$ MPa.

Zero turgor in *C. mertensiana* at similar $\psi_{\pi+\tau}$ values was measured in the field studies. Field measurements of *C. tetragona* indicated a maintenance of positive turgor at much lower $\psi_{\pi+\tau}$ values than these laboratory results. This may reflect different growing conditions or osmotic adjustment in response to stress. Laboratory plants were subjected to uniform conditions and no water stress. Field plants were exposed to more variable conditions and some water stress may have occurred even though measured soil water potentials were seasonally high. Osmotic adjustment has been shown to occur in other species in response to water stress (Jones and Turner 1978).

Negative turgor potentials were measured in both the laboratory and field studies, but whether this is a real phenomenon or simply a technique artifact is unclear. Negative turgor has been reported for a wide range of species (Kreeb 1963, Johnson and Caldwell 1976, Wilkinson 1977, Maxwell and Redmann 1978) but theoretical models are in disagreement over its possible existence (Warren Wilson 1967; Noy-Meir and Ginzburg 1967, 1969; Acock 1975; Tyree 1976).

Estimated values of the matrix-bound water content, expressed as a decimal part of the tissue water content at full turgor, are 0.24-0.26 for *C. tetragona* and 0.43-0.44 for *C. mertensiana*. Since most of the matrix-bound water in tissues probably occurs in the cell walls (Boyer 1967), this suggests that *C. mertensiana* has a higher proportion of structural tissue (i.e. greater sclerophylly) than *C. tetragona*. Acock (1975) suggests that this matrix-bound water, which constitutes the major part of the cell wall water, is not available to buffer cells against water loss. The elastic properties of cell walls are largely responsible for the partitioning of component potentials with changes in R. Cells with more elastic walls tend to decrease in volume and maintain relatively constant ψ_p over a wide range of R but with a concomitant large decrease in $\psi_{\pi+\tau}$. Cells with more rigid walls tend to decrease less in volume and show a large decrease in ψ_p while $\psi_{\pi+\tau}$ remains relatively constant. Walter (1931) referred to plants with elastic cell walls as hydrolabile (i.e. turgor stable) and plants with rigid cell walls as hydrostabile.

Estimates of cell wall elasticity (ε) were obtained from the change in ψ_p relative to the change in R between full turgor and zero turgor from the regression lines in Fig. 37. The calculated value from bulk tissue ψ_p for current leaves of *C. tetragona* was 0.98 MPa. Calculated values for old leaves of *C. tetragona* and current and old leaves of *C. mertensiana* were 3.52, 4.26, and 2.41 MPa, respectively. Although greater errors are involved in estimates from intracellular ψ_p , the results are theoretically more correct. The calculated values from intracellular ψ_p were 3.43 MPa for current leaves of *C. tetragona* and 6.15-6.50 MPa for the other tissues. Current leaves of *C. tetragona* have cells with relatively elastic walls and are hydrolabile, whereas the other leaves have cells with relatively rigid walls and are hydrostabile.

Winter Water Relations

Water contents, water potentials, component potentials, and xylem pressure potentials were measured in *Cassiope* at Sites 1 and 2 and at the *Dryas* transplant microsite in late winter, 1974-75, and in late fall and early winter, 1975. Microsites were selected to examine the affect of exposure versus winter snow cover on the water status of *Cassiope* through the winter.

Water contents measured on 28 September, 1975, were similar in both species at all microsites (230-240%, fresh weight as per cent of dry weight), and differed little from summer values (Table 19). Leaf water potentials were high (>-0.9 MPa) and ψ_p was high (>0.9 MPa). By 2 November, 1975, snow had accumulated in most microsites. Plants buried beneath the snow had similar or higher leaf hydration than in September, but *C. tetragona* tended to have lower water contents than *C. mertensiana*. *Cassiope tetragona* at exposed microsites had significantly lower water contents than snow covered plants. The presence of only 2 cm snow above shoots

TABLE 19. WATER RELATIONS PARAMETERS OF CASSIOPE AT VARIOUS MICROSITES IN LATE WINTER, 1974-75, AND LATE FALL AND EARLY WINTER, 1975. WATER CONTENTS ARE FRESH WEIGHTS AS PERCENT OF DRY WEIGHTS. SNOW COVER ON SAMPLE DATES AND CI.95 ARE INDICATED.

	SITE 1				SITE 2					DRYAS TRANSPLANT MICROSITE			
	C. MERTENSIANA	C. TETRAGONA			C. MERTENSIANA	C. TETRAGONA				C. MERTENSIANA		C. TETRAGONA	
	DEEP SNOW	DEEP SNOW	MODERATE SNOW	EXPOSED	DEEP SNOW	DEEP SNOW	MODERATE SNOW	LITTLE SNOW	EXPOSED	PROTECTED LEAVES	EXPOSED LEAVES	PROTECTED LEAVES	EXPOSED LEAVES
28 SEPT. 1975													
	(0 cm)		(0 cm)		(0 cm)		(0 cm)						
WATER CONTENT	244 ± 4%		233 ± 13%		231 ± 8%		234 ± 3%						
Ψ_L	-0.66 MPa		-0.91 MPa		-0.88 MPa		-0.72 MPa						
$\Psi_{\pi+\tau}$	-1.62 MPa		-2.15 MPa		-1.82 MPa		-1.73 MPa						
Ψ_P	0.96 MPa		1.25 MPa		0.94 MPa		1.01 MPa						
2 NOV. 1975													
	(50 cm)		(20 cm)	(0 cm)	(50 cm)	(25 cm)	(10 cm)		(0 cm)			(2 cm)	
WATER CONTENT	247 ± 17%		228 ± 4%	212 ± 8%	251 ± 9%	245 ± 20%	231 ± 12%		214 ± 6%			228 ± 19%	
Ψ_{XPP}	<-6.5 MPa		<-6.5 MPa	<-6.5 MPa	<-6.5 MPa	<-6.5 MPa	<-6.5 MPa		<-6.5 MPa			<-6.5 MPa	
22 NOV. 1975													
	(110 cm)	(90 cm)	(30 cm)	(0 cm)	(75 cm)	(35 cm)	(15 cm)	(0 cm)				(2 cm)	
WATER CONTENT	239 ± 13%	214 ± 23%	214 ± 12%	169 ± 10%	226 ± 17%	228 ± 7%	219 ± 10%	179 ± 6%				200 ± 17%	
Ψ_L	-1.28 MPa		-1.97 MPa		-0.55 MPa		-1.63 MPa						
$\Psi_{\pi+\tau}$	-2.49 MPa		-4.84 MPa		-2.77 MPa		-3.37 MPa						
Ψ_P	1.21 MPa		2.87 MPa		1.72 MPa		1.74 MPa						
Ψ_{XPP}	-1.10 ± 0.40 MPa	-2.22 ± 0.50 MPa	-2.93 ± 0.50 MPa	-4.85 ± 0.94 MPa	-1.55 ± 0.82 MPa	-3.92 ± 0.61 MPa	-2.89 ± 0.23 MPa	-3.73 ± 1.23 MPa				-4.01 ± 1.75 MPa	
24 APRIL 1975													
	(175 cm)	(175 cm)	(125 cm)	(0 cm)	(140 cm)		(100 cm)	(3-5 cm)	(0 cm)	(2 cm)	(0 cm)	(2 cm)	(0 cm)
WATER CONTENT	232 ± 5%	220 ± 10%	203 ± 3%	173 ± 9%	254 ± 10%		196 ± 11%	172 ± 11%	161 ± 6%	204 ± 17%	142 ± 4%	171 ± 25%	138 ± 7%
Ψ_L	-3.04 MPa		-6.41 MPa										
Ψ_{XPP}	-2.46 to <-4.5 MPa	<-6.5 MPa		<-6.5 MPa	-0.56 to -5.8 MPa		<-6.5 MPa	-5.1 to <-6.2 MPa	<-6.5 MPa	-4.1 MPa		<-6.5 MPa	

of *C. tetragona* in the *Dryas* transplant microsite helped maintain higher water contents. Xylem pressure potentials were <-6.5 MPa in plants of both species at all microsites.

By 22 November, 1975, water contents had declined in both species at all microsites. *Cassiope tetragona* again tended to have lower water contents than *C. mertensiana* in snow covered microsites, although differences were generally not significant. Snow covered plants had high ψ_L (-0.55 to -1.63 MPa) and ψ_p (1.21 to 2.87 MPa), and low $\psi_{\pi+\tau}$ (-2.49 to -4.84 MPa). Xylem pressure potentials were variable and generally lower than ψ_L. *Cassiope tetragona* in exposed microsites had significantly lower water contents (169-179%) and ψ_{xpp} (-3.73 to -4.85 MPa) than snow covered plants.

The data from 24 April, 1975, show the water status of *Cassiope* in late winter after a fall and early winter of desiccating conditions in exposed microsites. These results are from a different winter season than that reported above, and should not be considered as following in sequence.

Water contents of *C. mertensiana* were high (232-254%) at microsites with deep snow cover, but ψ_L was low (-3.04 MPa) and ψ_{xpp} was extremely variable (-0.56 to -5.8 MPa). *Cassiope tetragona* had lower water contents than *C. mertensiana* at all microsites. Tissue hydration of *C. tetragona* was inversely related to snow cover, and ψ_L and ψ_{xpp} were low at all microsites. Exposed plants of *C. tetragona* had low water contents (161-173%) and were severely dehydrated. Exposed shoots of both species at the

Dryas transplant microsite had very low water contents (138-142%) and appeared dead. Living shoots that were protected by only about 2 cm of snow had water contents higher than exposed shoots but lower than those at moderate to deep snow microsites.

The water relations of Cassiope are highly influenced by winter snow cover. Early snow cover permits the maintenance of high leaf hydration in both C. mertensiana and C. tetragona in their normal habitats, but all parameters tend to decline in both species through the winter. Cassiope mertensiana is covered by early and deep snow and does not normally experience dehydration. Cassiope tetragona is found in microsites of more variable snow cover, and tissue dehydration is directly related to exposure. Severe desiccation damage to C. tetragona in exposed microsites was noted on 24 April, 1975, (see Transplant Section) when water contents were 160-170%. Exposed shoots of both species were killed when water contents fell to ca. 140%. Shoots of C. mertensiana covered by about 2 cm of snow at the Dryas transplant microsite had high water contents (204%). The maintenance of higher water contents in C. mertensiana than in C. tetragona appears related to differences in both microsite conditions (normal habitats) and the physiology of the species. Reduced levels of hydration in C. tetragona may give it more tolerance to dehydration or low temperatures. The severe desiccation damage to protected shoots of C. mertensiana in the Dryas transplant microsite (see Transplant Section) suggests that C. mertensiana may be unable to tolerate dehydration to the same level as C. tetragona. The results also suggest that tissue damage to C. mertensiana described as due to desiccation may, in part, be due to low temperature injury and low temperature-induced dehydration.

Transplants

Transplants in the exposed Dryas and C. tetragona microsites were examined throughout the fall and early winter, 1974. By late December, plants appeared dehydrated and showed a slight browning of exposed leaves. Potentially desiccating conditions existed in early winter with temperatures above normal and a light snow cover. The minimum temperature to which plants were exposed was -17°C. By late April, 1975, most exposed plants showed severe injury. Exposed shoots, particularly those of C. mertensiana, were bright red in color, and damage appeared similar to that in cold hardiness tests (Figs. 38 and 39). Plants had been exposed to below-normal temperatures in January (to -33°C), and low temperature injury may have occurred. The exact timing of the stressful period was difficult to determine and the appearance of tissue damage may have been delayed.

Micro-patterns of snow accumulation around plant clumps indicated that exposure to desiccating conditions was the primary cause of injury to C. tetragona. Shoots covered by only 2-3 cm of snow were not insulated from low

A

B

Figure 38. The Dryas (a) and C. tetragona (b) transplant microsites. The red coloration of C. mertensiana plants (Cm) is largely due to severe desiccation the preceeding winter. Photographs taken in August, 1975.

COLOURED PICTURES
Images en couleur

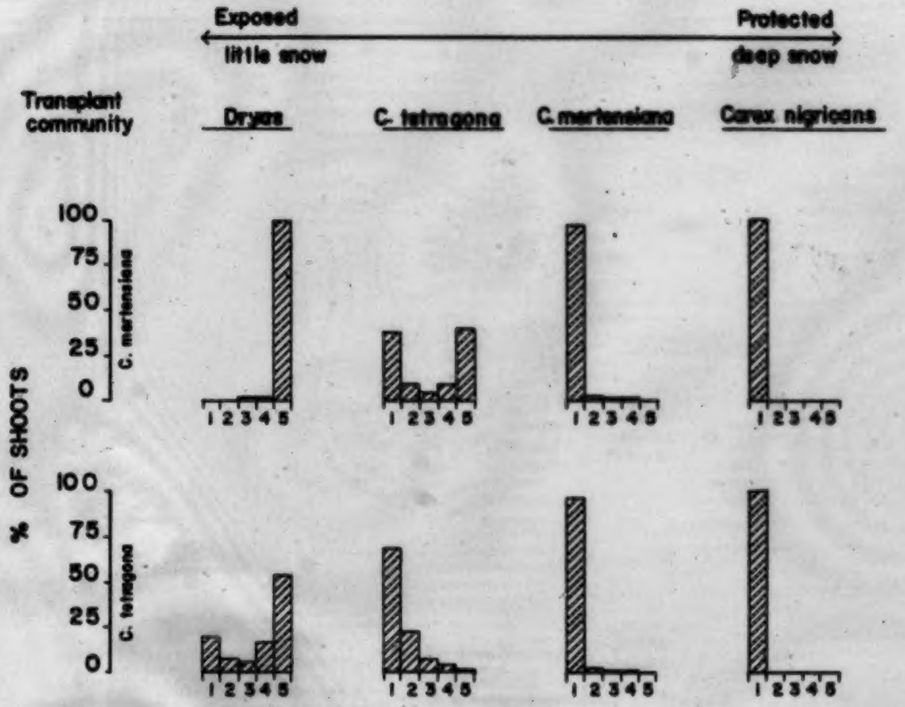
Figure 39. Close up of C. mertensiana (a) and C. tetragona (b) plants in the Dryas transplant microsite. Desiccation injury to C. mertensiana was extensive. Injury to C. tetragona was largely confined to the top, canopy shoots that projected above the snowpack. Photographs taken in August, 1975.

COLOURED PICTURES
Images en couleur

temperatures, but were protected from desiccating conditions and showed reduced levels of injury. Damage to C. mertensiana was more extensive. Although tissue damage was broadly correlated with the relative exposure of shoots, protected shoots also showed extensive damage. The timing and physical appearance of injury in C. mertensiana suggests the involvement of low temperature injury and low temperature-induced dehydration.

Desiccation injury to C. mertensiana was significantly greater (at P<0.01) than to C. tetragona in the Dryas and C. tetragona transplant microsites (Fig. 40). In the Dryas transplant microsite, nearly 100% of the shoots of C. mertensiana were killed while 25% of the shoots of C. tetragona showed slight or no damage. Injury to both species was less in the C. tetragona transplant microsite. In C. mertensiana, 40% of the shoots were killed and 47% showed slight or no damage. In C. tetragona, only 1% of the shoots were killed and 90% showed slight or no damage. Injury to both species was minor in the C. mertensiana transplant microsite, and 99% of the shoots of both species showed slight or no damage. No injury occurred in the Carex nigricans transplant microsite. Shoots of both species that sustained the greatest damage were located on the windward side of the plant clumps and at the tops of the canopy,about 2-3 cm above shoots that displayed slight or no damage.

Desiccation injury to plants along the transects at Sites 1 and 2 was directly related to the relative exposure



T value	6.04	5.61	-1.00	0
	P <0.01	P <0.01	NS	NS

Category

1 : No injury

2 : Slight injury, browning of apical leaves

3 : Moderate injury, leaves on one side of stem brown

4 : Severe injury, all leaves brown except protected buds and apices

5 : Tissue completely dead

Figure 40. Percentage of shoots of transplants showing varying degrees of winter desiccation (1974-75). The T-test (paired data, n = 6) was performed on the mean differences of categories 1 - 3.

of the microsites (Fig. 41). Cassiope mertensiana at Site 1 showed slight injury at the more exposed end of the community. At Site 2, all C. mertensiana microsites were very protected and no injury occurred. Cassiope mertensiana is found naturally only in very protected microtopographic areas that accumulate early and deep snow and plants are thus not normally subjected to desiccating conditions. Cassiope tetragona showed greater desiccation injury at both Sites and all microsites due to the greater exposure of these areas. In the C. tetragona community ca. 80 m along the transect at Site 2, 8% of the shoots showed moderate to severe damage. This indicates that desiccating conditions existed in early winter before deep snow accumulated at this microsite. Desiccation injury to C. mertensiana and C. tetragona in their natural habitats did not differ significantly from the transplants in the same general locations.

The survival of the transplants was measured four years after transplanting (Fig. 42). Shoots that were red in color after the first winter had long since turned grey and considerable wind erosion of the plant clumps had occurred in the Dryas transplant microsite. Shoot mortality was greater after four years than after one winter at all microsites. Cassiope tetragona showed significantly greater survival (at $P<0.01$) in the Dryas transplant microsite, but C. mertensiana showed significantly greater survival in both the C. mertensiana and Carex nigricans transplant

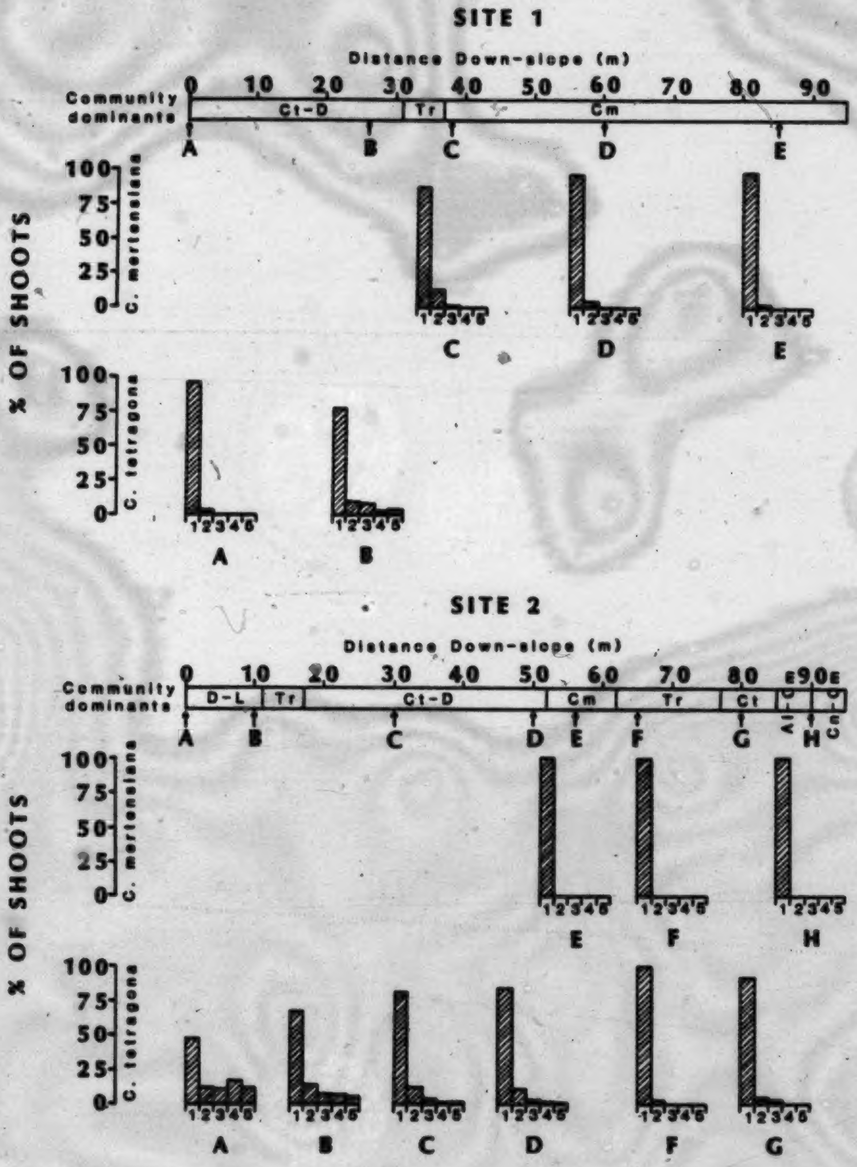
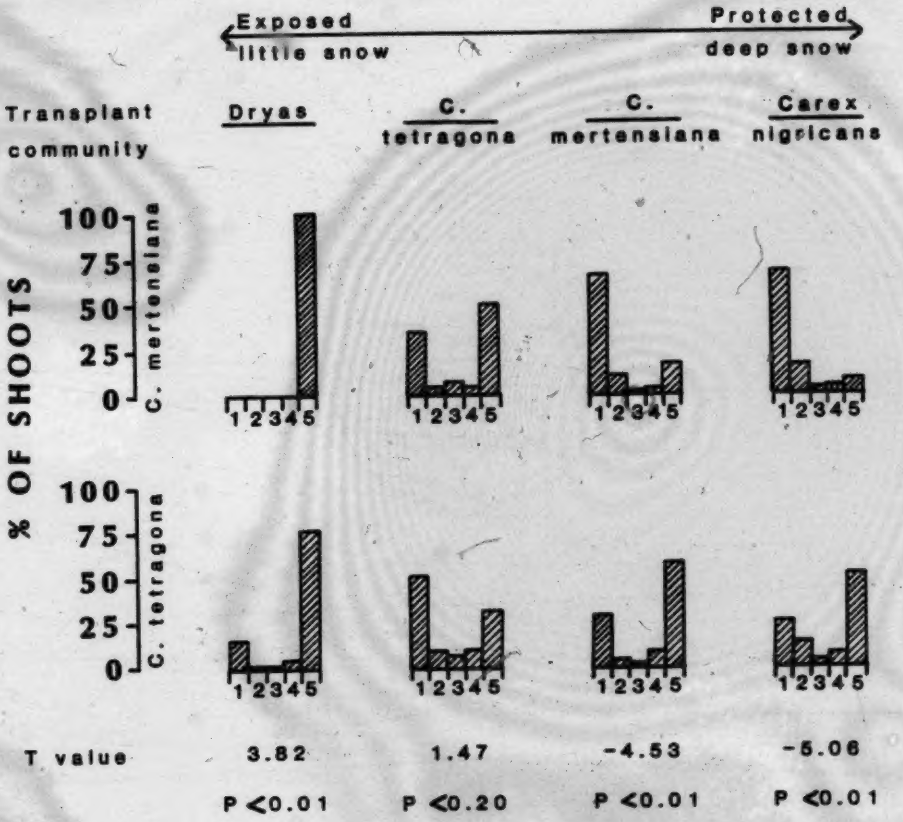


Figure 41. Percentage of shoots of plants along the transects at Sites 1 and 2 showing varying degrees of winter desiccation (1974-75). See Fig. 40 for injury scale and Figs. 10 and 11 for topographic profiles.



Category

1 : Healthy shoots

2 : Slight injury

3 : Moderate injury, *ca*. 50% of shoot dead

4 : Severe injury, all dead except protected parts

5 : Shoots completely dead

Figure 42. Percentage of shoots of transplants showing varying degrees of vitality in 1978, four years after transplanting. The T-test (paired data, n = 6) was performed on the mean differences of categories 1 - 3.

microsites. The mortality of shoots (particularly C. mertensiana) in the Dryas and C. tetragona transplant microsites was directly related to the desiccation that occurred during the 1974-75 winter (see Fig. 40). The mortality of shoots in the C. mertensiana and Carex nigricans transplant microsites was not related to desiccation, but rather the ability of the plants to survive in these late snow release microsites. However, the unavoidable root pruning of transplants that occurred at the time of establishment may have reduced plant vigor or "competitive ability" in the subsequent years.

Laboratory Simulation of Winter Desiccation

Simulated desiccation resulted in a very rapid loss of water and decline in ψ_L and ψ_p in both species (Fig. 43). The rate of decline of ψ_L tended to be greater in C. mertensiana although differences were not significant due to small sample size. Day 3 values are estimates due to the inaccuracy of psychrometric determinations at these low values; ψ_p probably dropped to 0 MPa before day 3. Water content of C. mertensiana was initially lower than C. tetragona (but not significant) and showed a more rapid rate of decline up to day 3. Water content of C. mertensiana was significantly lower than C. tetragona between days 3 and 6. Experimental results between days 3 and 6 approximated the minimum ψ_L and water contents measured in the field for exposed shoots (Table 19). Cut shoots sampled on day 4 and transferred to sand cultures failed to survive as did

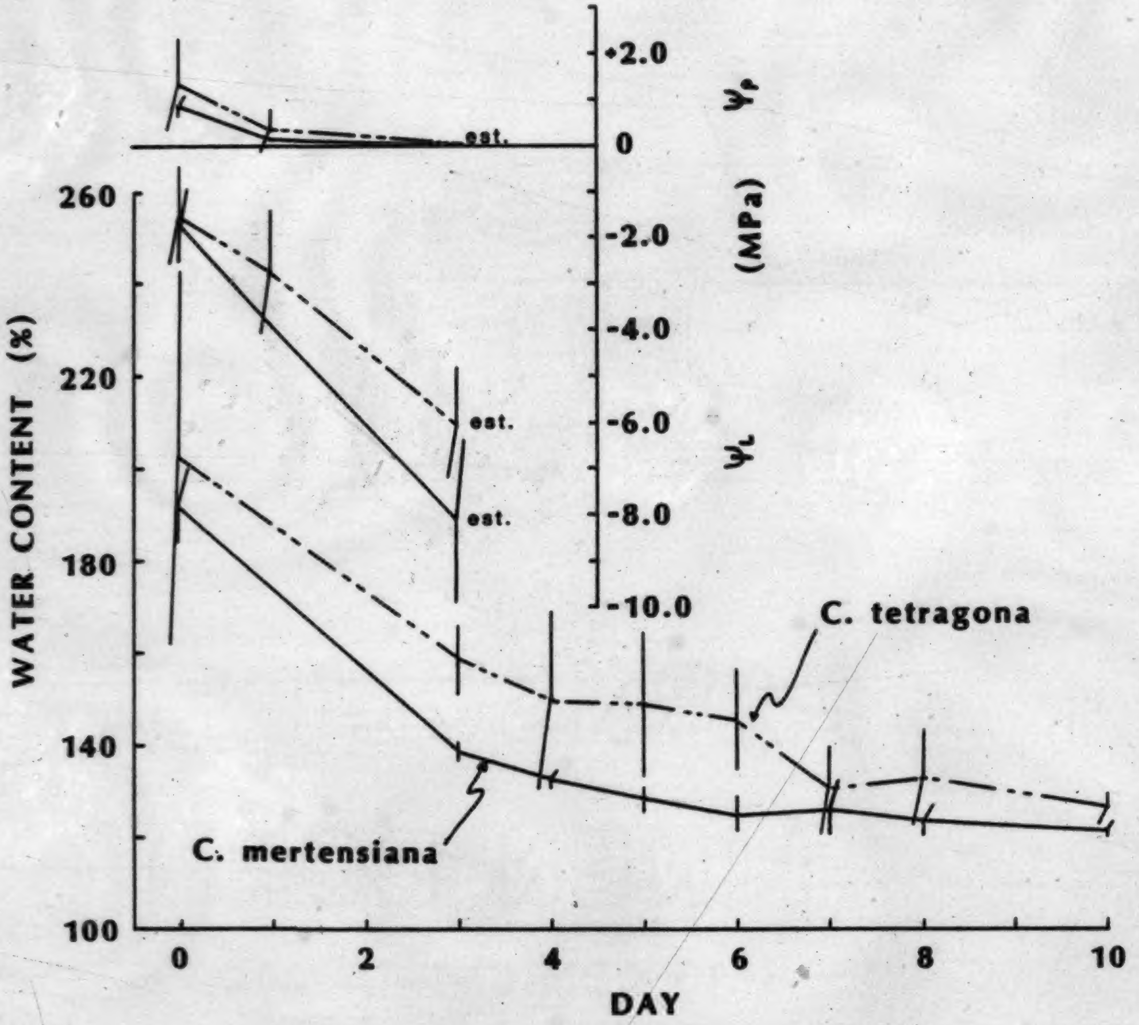


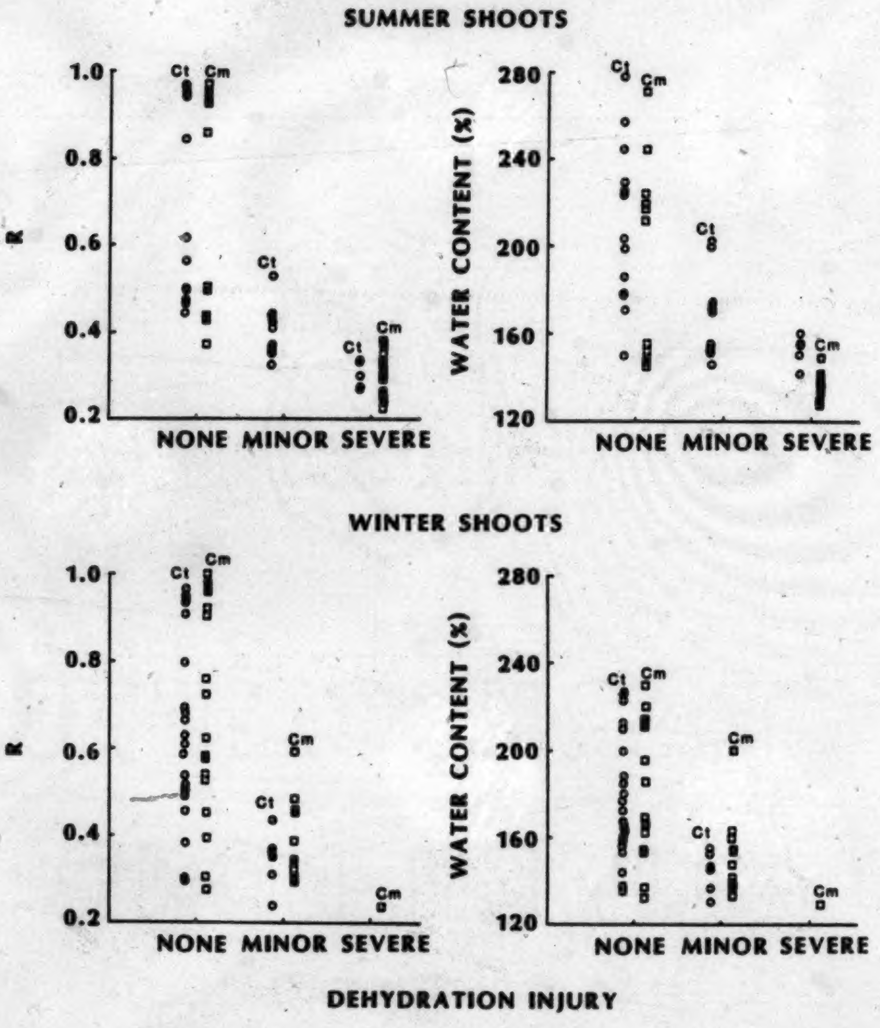
Figure 43. The decline of water content (fresh weight as per cent of dry weight), Ψ_L , and Ψ_P in C. mertensiana and C. tetragona exposed to simulated winter desiccation. CI.95 are indicated; est. = estimated.

severely dehydrated intact shoots on field plants. The simulated conditions (temperature and VPD) were more rigorous than occurred during mid winter in the field, but did approximate that which could occur during early and late winter. The results indicate that severe dehydration occurs in both species when exposed to intense and prolonged periods of desiccating conditions. The results also suggest that dehydration occurs more rapidly in C. mertensiana than in C. tetragona.

Dehydration Injury of Cut Shoots

Species differences in observable injury at various dehydration levels were not pronounced (Fig. 44). Minor injury to summer C. tetragona shoots was observed at R<0.5 and water contents <200%. Minor injury to C. mertensiana was not clearly distinguishable. Severe injury to both species was observed at R<0.35 and water contents <150 -160%. Winter shoots of both species were able to tolerate lower hydration levels. Minor injury to both species was observed at R<0.5 and water contents <160%. Severe injury was observed in one C. mertensiana shoot at R=0.24 and a water content of 130%. No severe injury to C. tetragona was observed at the hydration levels tested.

The data are inconclusive in separating the relative dehydration tolerance of C. tetragona and C. mertensiana. Observable injury after only 24 h rehydration may not reflect survival. Injury after only 6-12 h of deydration may be less severe than after prolonged exposure to low



Minor injury = observable damage

Severe injury = >50% of leaves discolored or killed

Figure 44. Observable dehydration injury of summer and winter _C. tetragona_ (Ct ○) and _C. mertensiana_ (Cm □) shoots as a function of water content (fresh weight as per cent of dry weight) and relative water content (R); n = 30.

hydration levels. Rates of dehydration to lethal limits may be more important to plant survival than absolute differences in tolerance of dehydration. However, these results are consistent with both the field studies (see Winter Water Relations Results) and the laboratory simulation of winter desiccation. In the latter, severe injury to both species occurred after prolonged exposures to water contents _ca_. 140-160%. The minor injury observed in winter shoots of both species after short exposures to these hydration levels could result in severe injury after prolonged exposures.

Cavitation in Frozen Stems

Freezing of stem sections of _Cassiope_ shoots in potometers increased the resistance of water movement through the stems after rewarming. This is evidence that freezing produced cavitation in the xylem sap. The 0-6 h water uptake rates of control and experimental shoots of both species were similar (Fig. 45). Rates decreased significantly immediately after freezing of experimental shoots and remained low for the following 21 h. The 7-10 h post-freezing rates were 35% (_C_. _mertensiana_) and 47% (_C_. _tetragona_) of the non-frozen controls. The 14-21 h recovery rates were 57% (_C_. _mertensiana_) and 49% (_C_. _tetragona_) of the non-frozen controls. This was due to a gradual decrease in the uptake rates of the control shoots and not to an increase in the uptake rates of the experimental shoots.

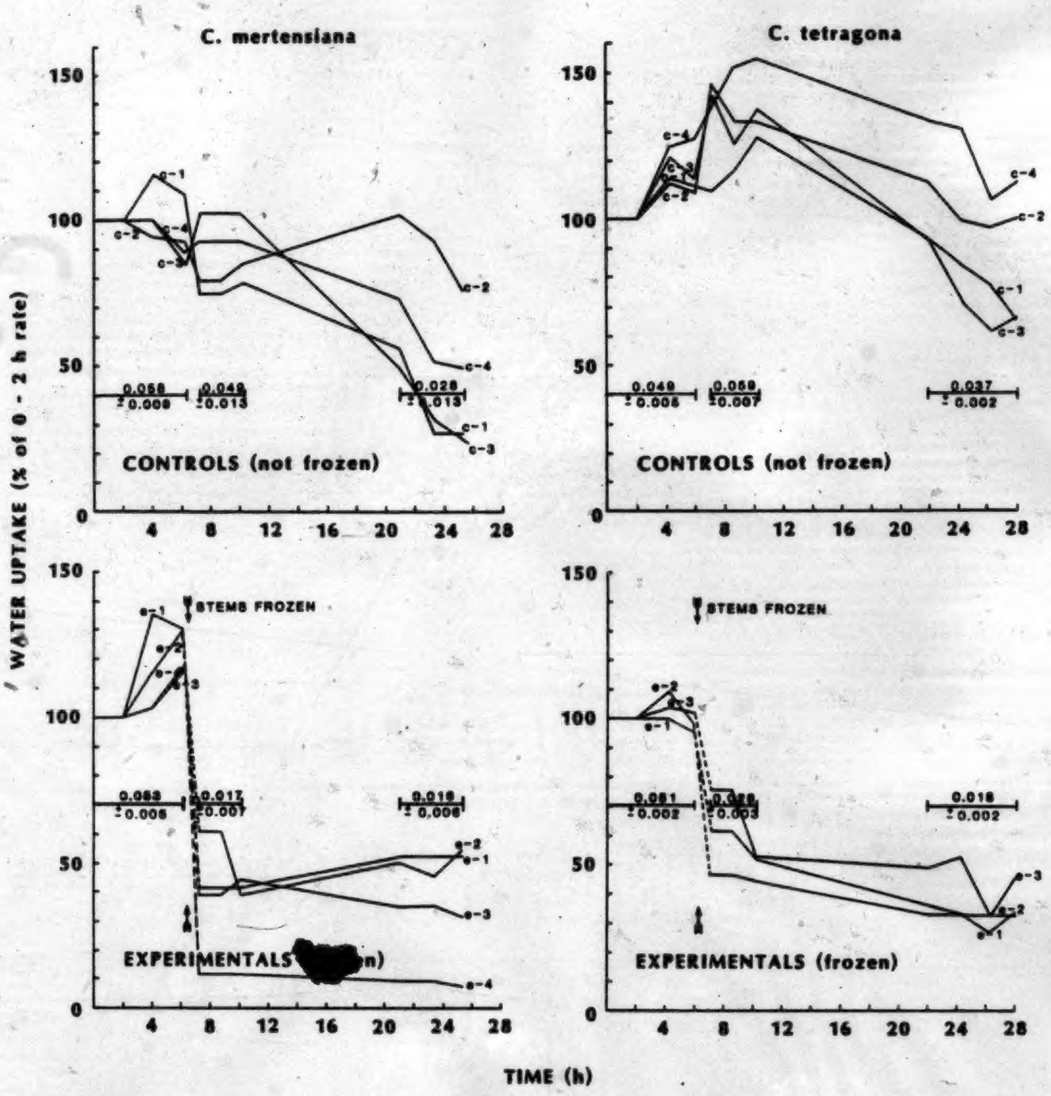


Figure 45. Water uptake of Cassiope shoots in potometers as a function of time and cavitation. Uptake is expressed as per cent of initial 2 h rate. A 2 cm stem section of experimental shoots was frozen with dry ice for 15 min at ca. 6 h. Values listed are rates of water uptake (g H_2O · g fresh wht^{-1} · h^{-1} ± CI.95) for the time periods indicated.

The in situ freezing of stem sections of Cassiope shoots on intact plants also indicated that freezing produced xylem sap cavitation. The ψ_{xpp} of pre-freezing and post-freezing controls of both species were similar (Table 20). Experimental shoots that had been frozen had significantly lower ψ_{xpp} than control shoots. This is evidence that cavitation occurred, disrupting the xylem water column. The lower ψ_{xpp} of cavitated shoots may be due to a combination of the presence of gas bubbles in the xylary vessels and a water deficit imposed on the plant tissues above the frozen sections.

The occurrence of cavitation has been reported in other heath species (Hammel 1967, Wilkinson 1977). Wilkinson (1977) found ψ_{xpp} to be erroneously low during the winter in Ledum groenlandicum and interpretated this as due to xylem sap cavitation. Similar results were found in this study (Table 19). The low ψ_{xpp} measured in the field during the winter indicates that xylem sap cavitation frequently occurs in Cassiope. Thus, winter measurements of ψ_{xpp} do not accurately reflect ψ_L . Cassiope may be exposed to tissue water deficits during the winter as a result of xylem sap cavitation.

Table 20. The ψ_{xpp} of *C. mertensiana* and *C. tetragona* shoots before and after freezing *in situ*. A 2 cm stem section of experimental shoots was frozen with dry ice for 15 min and post-freezing readings taken at 22 h. CI.95 are indicated. The T-test was performed on post-freezing control and experimental data.

Species	Pre-freezing Time 0 h	Post-freezing Time + 22 h		
	Control	Control (Not Frozen)	Experimental (Frozen)	T value (Unpaired Data)
C. mertensiana				
ψ_{xpp}^{MPa}	-0.88 ± 0.11 $n = 10$	-0.93 ± 0.14 $n = 6$	-3.84 ± 0.86 $n = 4$	-12.95 $P<0.001$
C. tetragona				
ψ_{xpp}^{MPa}	-0.91 ± 0.08 $n = 5$	-0.93 ± 0.06 $n = 5$	-1.91 ± 0.26 $n = 4$	-13.00 $P<0.001$

V. DISCUSSION

A. Microenvironments

Cassiope mertensiana and *C. tetragona* experience seasonally different microenvironments at treeline in the Canadian Rocky Mountains. Their local distribution is directly related to microtopography which controls winter snow depth and which consequently influences both winter and summer conditions. While both species are chionophilic, their niche separation along gradients of winter snow cover and snow release can partially be explained by physiological differences in plant water relations and cold hardiness. These differences may also influence the overall geographic distribution of the species.

Cassiope mertensiana is restricted to protected, leeward slopes below treeline or concave microsites in the low alpine zone. Late autumn and early winter snowfalls are redistributed by wind and accumulate differentially in these depressional areas. Plants are usually completely snow covered by mid to late October. *Cassiope tetragona* is found in more exposed convex to concave microsites where snow accumulations greater than plant canopy height (15 cm) are delayed 3-6 wk. *Cassiope mertensiana* is always covered by early winter snow but *C. tetragona* is never completely covered at this time.

Low autumn snowfalls occur with a high frequency in the more continental regions of the Cordilleras such as Jasper National Park (Janz and Storr 1977). This results in great year to year variability in the time of arrival of continuous snow cover and the air temperatures to which C. tetragona plants are exposed in early winter. Plants of exposed microsites frequently experience either desiccating conditions or air temperatures <-25 to -30°C. The time of arrival of snow cover in C. mertensiana habitats is less variable and plants are rarely exposed to either desiccating conditions or to low air temperatures <-15 to -20°C.

Total snow accumulation in C. mertensiana habitats is >1.5-2 m, >200% that in normal C. tetragona habitats. However, C. tetragona occasionally occurs in areas of deep snow cover, but such microsites are invariably downslope of large snow drifts and exposed in early winter. Winter temperatures are mild for snow covered plants of both species. Beneath a deep snow cover, C. mertensiana shoots at +10 cm and roots at -10 cm experience minimum temperatures of about -2 to -4°C. Beneath a more shallow snow cover, C. tetragona plants experience minimum temperatures of about -6 to -8°C.

Snow depth in Cassiope habitats influences snow duration which in turn influences the summer conditions to which plants are exposed. Cassiope tetragona normally melts out in mid June. However, in years of light winter precipitation, shoots of plants in exposed microsites may project above the snow in May and be exposed to high temperatures and VPD's when soils are still frozen. Snow release of C. mertensiana habitats usually occurs in early

July, about 3 wk after *C. tetragona* habitats are snow free. The start of snow release in *C. mertensiana* habitats is less variable due to consistantly greater snow accumulations, but it may extend longer for the same reason.

Soil temperatures in habitats of both species rise to near 0°C at least one month prior to snow release and some water uptake may occur in snow covered plants. However, after snow release of *C. tetragona* habitats in mid June, low soil temperatures (<2°C) persist due to the percolation of melt waters. Although air temperatures during this period are generally low because the melting snow serves as a heat sink, *C. tetragona* may be exposed to air temperatures >15°C and VPD's >1.0 kPa while water uptake is limited by low soil temperatures. Melt out of *C. mertensiana* habitats in early July coincides with the period of maximum temperatures ($\bar{X}$ daily *ca*. 10°C) and radiation ($\bar{X}$ daily *ca*. 18.5 - 21.3 $MJ\bullet m^{-2}\bullet d^{-1}$). Soil temperatures rise rapidly after snow release in *C. mertensiana* habitats and the rise is synchronous in *C. tetragona* habitats. Maximum soil temperatures occur in July but are high throughout the growth period of July and August. Maximum soil temperatures are higher in *C. tetragona* habitats (*ca*. 16-20°C at 0 cm and 6-8°C at -10 cm) than in *C. mertensiana* habitats (*ca*. 18°C at 0 cm and 5-6°C at -10 cm). The lower soil temperatures in *C. mertensiana* habitats are due to less exposure to direct radiation (microtopographic depressions) and the insulating effects of greater plant cover, soil moisture, and soil organic matter.

The late snow release of Cassiope habitats delays the summer decline in soil moisture. In 1975, summer precipitation was near normal and mean soil water potentials at all microsites and depths were >-0.03 MPa and no values were recorded <1.50 MPa. Soil moisture tended to be slightly higher in C. mertensiana habitats. Drier soils were noted in years of below-normal precipitation (1973 and 1974) but quantitative data were lacking. Late season soil moisture stress may occur in Cassiope habitats in dry years. However, the later snow release of C. mertensiana habitats compared to more exposed microsites, provides a more favorable summer soil moisture regime and reduces the potential of late-season stress.

Soil moisture depletion is retarded by frequent summer precipitation (1 day in 3). Although great variability was noted in total monthly precipitation (<20 mm to 107 mm) during the study years, dry periods longer than ten days were rare. Summer snowfalls (17% of summer precipitation) are differentially deposited in C. mertensiana depressional areas and may retard soil moisture depletion in such microsites.

Cassiope plants are exposed to daily air temperatures ca. 5-15°C during July and August. The absolute temperature range recorded during these months was -3 to 25°C. Mean daily temperatures tended to be slightly higher and maximum temperatures significantly higher (1-2°C) at the lower elevation Site. Temperatures within plant canopies can be several degrees above ambient on calm, sunny days. However, plant canopy temperature differences between adjacent C. mertensiana and C. tetragona microsites are small. While C. tetragona microsites are exposed to more direct radiation, this results primarily in greater soil heat flux. Higher windspeeds within the more open plant canopy of C. tetragona result in greater air mixing and reduce canopy temperatures. Thus, temperatures are frequently slightly higher within the canopy of C. mertensiana.

Leaf temperatures up to 9°C above ambient air temperatures were measured in both species on sunny days. Leaf to air temperature differences were small on cloudy or windy days. Plants such as Cassiope that have erect branches and small, sessile leaves which are closely appressed to stems have a low boundary layer resistance and rapid convective heat loss (Gates and Papian 1971). This contrasts with mat-forming and cushion plants where leaf temperatures are frequently elevated 20°C or more above ambient (Courtin and Mayo 1975).

The adaptive advantage of the canopy and leaf characteristics of Cassiope and other heath species is unclear. Yates (1981) compared the optical properties of heathland communities in Australia and found that short wave reflectivity (albedo) was less in small leaved species with low canopy heights and this led to an increase in the absorption of solar radiation by the plant canopy as a whole. The more dense plant canopy of C. mertensiana may function optically as well as through wind attenuation in providing a more suitable thermal regime for photosynthesis and growth. This would be advantageous in microsites with a short growing season due to late snow release, but only if soil moisture was sufficient to reduce water stress. Radiational heating of C. tetragona would be reduced by the more open plant canopy, but this may be partially offset by leaf coloration. Leaves of C. tetragona have greater pigmentation, i.e. are relatively darker, than C. mertensiana. This is important, at least during snow release, because it results in elevated leaf temperatures and local thawing around shoots. The spirally arranged leaves of both species may result in a greater efficiency of radiation absorption, particularly in northern latitudes with low sun angles.

Vapor pressure deficits were frequently high during the summer and were directly correlated with air temperature. Maximum VPD's were about 2.0 kPa during July and August and averaged 0.13 kPa higher at Site 1. Although VPD's within plant canopies tended to be lower than in the ambient air, actual vapor pressure gradients between leaves and the air probably exceed the reported values due to above ambient leaf temperatures.

B. Plant Growth and Reproduction

The variability of climatic conditions during the study years helped to more strictly delineate the range of microenvironmental conditions possible in *Cassiope* habitats and the factors restricting plant growth and survival. The *Cassiope* communities studied represent stable populations that have integrated and adjusted to long-term climatic fluctuations. Plants are old (30-50 yr or more) and reproduce aggressively in their normal habitats by long-lived rhizomes or adventituous rooting from decumbent shoots. The local populations may even represent clones with a long history of vegetative reproduction. Patterns of plant growth, soil development beneath plant clumps, and buried stems and rhizomes indicate both species have persisted in their present positions along mesotopographic gradients for long periods of time. The slow growth rates and conservative reproductive strategies of *Cassiope* do not allow rapid expansion into new habitats during short intervals of ameliorated climatic conditions, with the possible exception of seedling establishment in newly exposed, mesic sites. Edwards (1980) noted similar patterns in *C. mertensiana*-*Phyllodoce* communities on Mount Rainier. The mature phase of the heath communities was long lasting (7000-10,000 yr) and buried stems were estimated (C^{14}) at >6000 yr old. Pollen analysis indicated that the communities have not extended beyond their present topographic or elevational positions.

The present distributional patterns of *C. mertensiana* and *C. tetragona* are primarily dependent on the tolerances of mature plants rather than successful sexual reproduction.

For this reason, the latter was only cursorily examined. Both species flower abundantly and produce large quantities of small seeds which are readily wind dispersed into most habitats. Neither seed germination nor seedling establishment was observed for either species during this study.

Seed germination rates of heath species are often variable and low (Nichols 1934, Bliss 1958, Karlin 1978). Bliss (1958) reported 52% germination of *C. tetragona* after 26 d at 22°C in the light and no germination in the dark. Edwards (1980) reported 81% seed viability of *C. mertensiana*, but only 28% germination after 27 d in the light and no germination in the dark. *Cassiope* seeds probably do not possess long-term viability due to their small size and limited food reserves. Seed germination rates of ericaceous species decline rapidly with age (Karlin 1978) and viable seeds are uncommon in soil seed banks (Johnson 1975, Moore and Wein 1977).

Cassiope seedlings are extremely small and low growth rates maintain the seedling size for several years. Seedlings are sensitive to soil moisture stress due to the shallow penetration of radicles into the soil. Successful seedling establishment would apparently require favorable environmental conditions over several years. Substrates, soil moisture stress, and competition with vascular and moss species were shown to limit seedling establishment of *C. mertensiana* (Edwards 1980) and *Ledum groenlandicum* (Karlin

1978) in their natural habitats. Edwards (1980) observed successful seedling establishment of *C. mertensiana* on Mount Rainier only in open, stony habitats below large snowbanks. In the current study, small plants that had apparently established from seeds were observed colonizing new habitats, such as moraines or areas of late snow release, with reduced plant cover. All of these areas may have become open since the Neoglaciation due to climatic warming. Also, they all have abundant soil moisture at the surface and a low potential for seedling desiccation. The microenvironments and tolerances of seedlings are different from those of mature plants.

Sexual and vegetative reproduction of *Cassiope* are also under different environmental constraints at the mature plant level. Reproductive development and flower production are not directly linked to shoot growth or leaf production. Phenological patterns in *C. mertensiana* and *C. tetragona* are basically similar but influenced by snow release. Flower buds and shoots of both species are quiescent during most of the winter beneath the snow. Flower bud expansion normally begins after snow release in *C. tetragona* but prior to release in *C. mertensiana*. The initial period of inactivity in *C. tetragona* may be related to the generally low air and soil temperatures following snow release. However, environmental cues may also be involved. The start of flower bud expansion in both species lags by *ca*. 6-8 wk the rise of temperatures to near 0°C in the subnival plant environment.

This may initiate the translocation of substances involved in bud expansion. Peak flowering occurs earlier in C. tetragona (27-48 d after release) than in C. mertensiana (28-31 d after release), but flowering periods overlap. In both species, phenology is advanced in years or microsites of early snow release and delayed by late lying snow. Fruit maturation and seed production are reduced, especially in C. mertensiana, in microsites of late snow release and flowering.

Cassiope mertensiana and C. tetragona have a conservative growth strategy and appear well adapted to habitats of intermediate snow release. However, the evergreen habit imposes certain limitations related to winter survival and summer carbon balance that may exclude them from the two ends of the exposure gradient.

The evergreen habit of Cassiope differs in the manner of leaf maturation from that of many other evergreen heaths or conifers. Leaf and shoot primordia of the latter are protected by buds during the winter, display a flush of growth during the spring and summer, and reach maturity in time to withstand the rigors of the ensuing winter. The effect of poor growth conditions on tissue maturation and bud development in evergreen conifers at treeline is well documented (Tranquillini 1979). Incomplete cuticular development on leaves or late terminal bud formation makes these tissues highly susceptible to winter injury due to low temperatures or desiccation. In contrast, Cassiope produces no terminal buds, although the leaves which envelop the apex act as such (Böcher 1981). Leaf maturation occurs basipetally from the apex over a protracted period (Sørensen 1941). Leaves of both species are differentiated on the apex about 2 yr prior to expansion to full size. Growth during the summer involves the expansion to full size of a leaf set, the partial expansion of leaf primordia of the previous summer, and the differentiation of new primordia. Thus, environmental conditions over 3 yr influence subsequent growth increments. Leaves must overwinter in various states of maturity and the protection afforded by winter snow cover may be a requisite.

Shoot growth is synchronous in both species, except where delayed by late snow release. Cassiope tetragona has a quiescent period following snow melt that does not appear controlled by canopy microenvironments. Rapid growth begins when soil temperatures rise above ca. 2-5°C in C. tetragona habitats and 0.5-1.5°C in C. mertensiana habitats. Most shoot elongation occurs over a 5-7 wk period in July and August and coincides with maximum seasonal temperatures and radiation. Growth rates are low but consistent during this period. Canopy shoots of both species elongate ca. 5.5 mm/yr (mean of all microsites and years) and produce ca. 1 leaf pair/mm. Protected shoots frequently elongate >10 mm/yr. Shoot elongation ceases in late August and may be triggered by short days and fall hardening. Growth of C. mertensiana was reduced in microsites of early or late snow release or at higher elevations. Growth of C. tetragona was greater in microsites of early snow release. Growth of both species was greater in a year (1975) of early snow release, high temperatures in July, and high soil moisture.

Leaf longevity of Cassiope has functional importance related to summer carbon gains. Evergreen leaves are retained ca. 2-3 yr in C. tetragona and 5-7 yr in C. mertensiana in normal habitats. The greater proportion of photosynthetic tissue in C. mertensiana may give it a competitive advantage in areas with a shortened growing season. Leaf longevity is greater in both species in microsites of later snow release. In the High Arctic, severe summer environments limit leaf production in C. tetragona to ca. 2 leaf pairs/yr, but this is compensated for by extended leaf longevity (ca. 5 yr) (Bliss et al. 1977). This maintains a similar amount of photosynthetic tissue as measured in the current study, but leaf production and longevity differ considerably.

C. Photosynthesis

Among tundra species of different growth form, photosynthetic capacity appears to be inversely related to leaf longevity (Johnson and Tieszen 1976). Although evergreen dwarf shrubs maximize radiation interception during the growing season, CO_2 uptake and photosynthesis are often low (Hadley and Bliss 1964, Tieszen and Wieland 1975). This is in part due to leaf sclerophylly and increased leaf resistances which may be adaptions to moisture stress

(Courtin and Mayo 1975).

The slow growth of Cassiope is probably due to low photosynthetic rates. Johnson and Tieszen (1976) report the photosynthetic capacity of arctic (Alaska) C. tetragona as 9-10 mg $CO_2 \bullet g$ dry $wt^{-1} \bullet h^{-1}$ (at 15°C). This was 20-50% that of sympatric grasses and sedges, herbaceous forbs, and deciduous shrubs. The photosynthetic capacity of C. mertensiana has not been reported but is probably comparable, i.e. low. The delayed growth of C. tetragona suggests that early season carbon gains are allocated primarily to flower production, with later season gains going primarily to leaf production. Flowering and growth are more synchronous in C. mertensiana. The extended leaf longevity may be a compensation necessary to allow greater carbon gains during a shorter period.

D. Water Relations

Differences in the water relations of Cassiope suggest limitations to tissue survival and plant growth along the exposure gradient. Summer trends of midday ψ_L and $\psi_{\pi+\tau}$ are similar in both species, rising from a low at snow release to mid summer maxima and declining rapidly in the fall. Leaf water potentials and $\psi_{\pi+\tau}$ at snow release were ca. -2.0 to -3.5 MPa and -2.5 to -5.0 MPa, respectively. These low values do not necessarily indicate stress but rather reflect the overwinter storage of carbohydrates and lipids in old leaves and stems (Hadley and Bliss 1964). A similar pattern of storage occurs in non-heath species that maintain winter-green leaves (Bell and Bliss 1979), and contrasts with summer-green species where the roots and rhizomes are the primary storage organs (Mooney and Billings 1960). Leaf water potentials and $\psi_{\pi+\tau}$ increased gradually after snow release as storage reserves were utilized in flower and leaf production; mid summer maxima were *ca*. -0.5 to -1.0 MPa and -1.0 to -1.5 MPa, respectively. Leaf water potentials were always much lower than soil water potentials, indicating a high resistance to water uptake by the roots. *Cassiope tetragona* maintained diurnally constant ψ_p regardless of changes in ψ_L or environmental conditions. *Cassiope mertensiana* frequently showed a midday reduction in ψ_p indicating water stress, even though soil moisture was high.

These results are supported by other field and laboratory measurements which indicate that *C*. *tetragona* has a greater tolerance of water stress than *C*. *mertensiana*. Both species have high leaf resistances, in part due to the sclerophyllous leaves and stomatal location. The minimum measured leaf resistances were *ca*. 7-9 s/cm (potometers) and 1-2 s/cm (diffusive resistance porometer) for both species. The latter are comparable to values reported in other studies using a null balance porometer; Edwards (1980) measured 1.8 s/cm in *C*. *mertensiana* and Oberbauer and Miller (1981) measured 0.8 s/cm in *C*. *tetragona*. The stomata of both species are sensitive to levels of atmospheric moisture stress that occur on warmer days. Increasing VPD's cause an increase in the transpiration and leaf resistance of both species, but greater stomatal closure appears to occur in C. mertensiana. The increase in leaf resistance is due in part to changes in bulk leaf water status. The frequent reductions of ψ_p (often to near zero) in C. mertensiana would indicate stomatal closure and restrictions on CO_2 uptake and photosynthesis.

Measurements of field transpiration indicate that water loss is low but may be curtailed to a greater extent in C. mertensiana. Although transpiration rates (ca. 0.20-0.25 g $H_2O \bullet g$ dry $wt^{-1} \bullet h^{-1}$) and species differences were not significant, mean daily rates tended to be slightly higher and maximum daily rates 1.4 times higher in C. mertensiana than in C. tetragona. The low rates measured in Cassiope are similar to those reported for other evergreen Ericaceous dwarf shrubs at treeline (Stocker 1931, Pisek and Cartellieri 1934), but are lower than the rates of sympatric deciduous shrubs, forbs, and graminoids (Bliss 1960, Oberbauer and Miller 1981).

The differential stomatal response of C. mertensiana and C. tetragona can partially be explained by cell wall characteristics which influence the partitioning of component potentials with changes in water content. Old leaves of C. tetragona and current and old leaves of C. mertensiana have relatively rigid cell walls. Water loss is accompanied by a small decrease in cell volume and $\psi_{\pi+\tau}$, but a relatively large decrease in ψ_p . Current leaves of C. tetragona have more elastic cell walls and positive turgor is maintained at a lower water content. This appears responsible for the maintenance by C. tetragona of relatively constant turgor during the summer months in the field studies. Although both species possess sclerophyllous leaves with many xeromorphic features, the change in ψ_L with water loss, and the estimates of cell wall elasticity indicate they are mesophytic species and not adapted to extreme drought.

These results agree with other studies of the response of alpine species along mesotopographic gradients. Oberbauer and Miller (1979,1981) compared the water relations of evergreen shrubs, deciduous shrubs, forbs, and graminoids in different vegetation types and habitats around a snow patch in the Alaskan alpine tundra. The Cassiope tetragona zone had the greatest water stress (lowest water potentials) of all sites sampled. Cassiope tetragona had the lowest transpiration rate and highest leaf resistance, and reached the lowest ψ_{xpp} of all species measured.

Stomatal closure as a direct response to evaporative conditions of the atmosphere has been reported in a wide range of plants (Lange et al. 1971, Schulze et al. 1972, Hall et al. 1976, Sheriff 1977, Farquhar 1978). Mooney et al. (1965) found differences in the water requirements of California alpine herbaceous plants related to patterns of their local distribution. Plants of wet sites transpired more but displayed a greater midday reduction during periods of high VPD. Johnson and Caldwell (1975, 1976) compared the responses of four arctic and alpine species to atmospheric and soil moisture stress. All species exhibited stomatal closure with increasing atmospheric moisture stress at high soil water potentials. However, the wet site species exhibited small reductions in ψ_L and apparent hydropassive stomatal closure due to changes in bulk leaf water status. This resulted in a reduction of photosynthesis. The species with wider habitat ranges showed no significant declines in ψ_L with increasing VPD. The stomata may have responded directly to VPD and prevented water loss by partial stomatal closure. Photosynthesis was not as abruptly curtailed by increasing atmospheric or soil moisture stress as in the wet site species. Similar patterns of cell wall elasticity and partitioning of water potential and component potentials were found in C. mertensiana and C. tetragona as in the wet site and the wider ranging species, respectively. However, hydropassive reductions in stomatal aperture due to changes in bulk leaf water status appeared to occur in both species of Cassiope, but to a greater extent in C. mertensiana. The cell wall characteristics of C. tetragona may have abated reductions in ψ_p and stomatal closure.

The characteristics of the summer water relations of Cassiope may relate to their survival ability in different microenvironments. Cassiope tetragona is able to maintain positive turgor necessary for cell wall expansion and shoot growth (Cleland 1967, 1971, Ray et al. 1972, Hsiao 1973) and more favorable internal conditions for photosynthesis with increasing atmospheric or soil moisture stress. Growth and photosynthesis of C. mertensiana is favored in more mesic sites.

The winter water relations of Cassiope are regulated by the relative exposure of microsites and snow cover. Osmotic potentials decline in early fall and winter and are paralleled by a decline in ψ_L except in snow covered plants. This response is characteristic of evergreen Ericaceous shrubs and does not indicate water stress (Pisek 1956, Tranquillini 1963, Wilkinson 1977), but rather the overwinter storage of reserves or protoplasmic augmentation related to cold hardening (Siminovitch et al. 1968). High water contents (ca. 230%) and ψ_L (>-3.1 MPa) are maintained by C. mertensiana in normal habitats (i.e. deep snow accumulation microsites) through the winter. Plants are exposed to only short periods of desiccation prior to being snow covered. No desiccation injury of C. mertensiana was observed in its normal habitats. Xylem sap cavitation frequently occurs in early winter, but is usually alleviated beneath the snow. Cavitated plants are not subjected to stress conditions in the water-vapor saturated, subnival environment. Water uptake by roots does not occur during the winter months because soils are <-1° (Larcher 1957).

Cassiope tetragona experiences less favorable conditions in all but very deep snow accumulation microsites. Snow cover is delayed with respect to C. mertensiana habitats and plants may project above the snow in exposed microsites in mid winter, even in years of normal winter snowfalls. Exposed shoots experience xylem sap cavitation and severe dehydration with no potential for replacing lost water. Water potentials often drop to levels <-6.0 MPa but appear non-lethal, in contrast to C. mertensiana. In very exposed microsites, snow cover is periodic and plants dehydrate to water contents <ca. 160-170% and severe injury results. Desiccation damage to C. tetragona in its normal habitats is directly related to exposure. Minor desiccation damage can occur even in microsites of relatively early snow cover due to higher temperatures and VPD's in early winter.

Transplants of both species experienced severe desiccation and wind erosion of plant tissues in exposed Dryas habitats. Desiccation damage was greater in C. mertensiana and appeared to occur at higher water contents than in C. tetragona. Cassiope mertensiana also exhibited significantly greater tissue damage in the C. tetragona transplant microsite. The potential for desiccation in areas of low or variable snow cover excludes C. mertensiana from such sites. Edwards (1980) reported similar desiccation of C. mertensiana on Mount Rainier when shoots protruded above the snow all winter. The high mortality was explained on the basis of low leaf resistance under cold conditions, stomatal arrangement, and xylem sap cavitation.

Physiological and morphological factors are involved in the greater tolerance of C. tetragona to winter desiccation.

Laboratory experiments indicate that both species dehydrate rapidly when exposed to severely desiccating conditions. However, the rate of water loss is greater in C. mertensiana and plants are unable to survive at as low levels of tissue hydration as C. tetragona. Leaves of C. mertensiana frequently project at a slight angle away from the stem exposing stomates and a greater leaf surface to desiccation. Leaves of C. tetragona are more closely imbricate and dehydration tends to seal the abaxial groove and adaxial leaf surface. The shoot apex has many dense and active glands which secrete resinous material, helping to seal the young leaves and apex against water loss. Furthermore, these glands may function as hydathodes, absorbing and secreting water to the apical meristem (Böcher 1981). Severely desiccated shoots of C. tetragona often have undamaged immature leaves and apices, while damage to C. mertensiana is more total.

Field desiccated shoots of Cassiope were reddish-brown in color, resembling the desiccated needles of conifer krummholz (see Tranquillini 1979) or the winter browning of Calluna and other heath species (Watson et al. 1966). The traditional explanation for such damage has been the evaporative loss of water from exposed foliage when soils are frozen and uptake prohibited. However, it is often difficult to distinguish the cause of such damage because both drought and freezing may be involved (Tranquillini 1964, 1979). Increasing water stress that is reversible may be indistinguishable from irreversible dehydration that occurs after tissues are injured from other causes. Wardle (1981) demonstrated that first-year needles of *Picea engelmannii* developed typical desiccation-damage patterns after freezing experiments. The damage to *C. mertensiana* was more extensive and only broadly correlated with shoot exposure, suggesting that low temperature stress may have been involved.

E. Cold Hardiness

Cassiope mertensiana and *C. tetragona* develop a cold tolerance to levels below the minimum temperatures in their respective habitats. Summer plants of both species can tolerate temperatures to -10°C which is below minimum summer temperatures. Winter hardy *C. mertensiana* is injured by one hour exposure to -26°C and severely injured at -36°C. Winter hardy *C. tetragona* can tolerate these temperatures with little injury. Temperatures <-26°C frequently occur in exposed *C. tetragona* habitats in mid winter.

These results are consistent with other studies of evergreen Ericaceous shrubs and their habitat requirements. Tranquillini (1963, 1964) reported that *Rhododendron ferrugineum*, *Vaccinium vitis-idaea*, and *Erica carnea* were frost sensitive plants, hardy to only -20 to -24°C and thus limited to snow protected sites near treeline. Heath species of more exposed sites (e.g. *Loiseleuria procumbens*) were able to tolerate temperatures down to -36°C. Sakai and Otsuka (1970) determined the freezing resistance of alpine plants in Japan. Cassiope lycopodioides was the least hardy (-40°C leaf, -30°C stem) of all the plants sampled in winter, and is restricted to protected sites. Bieble (1968) measured the hardiness of many species in Greenland. Cassiope tetragona could tolerate -8°C for 24 h in the summer and -46°C for 0.5 h in the winter.

Low temperature is an important factor in determining plant distributions and has led to the evolution of cold hardy taxa in continental climates with severe cold and dry winters (Parker 1963, Sakai and Weiser 1973). Southern provenances of cold temperate and boreal woody species retain an inherent ability to harden although moderated by the timing of growth cessation in the fall (Scheuman and Schönbach 1968, Smithberg and Weiser 1968). Species of Salix now adapted to tropical regions also possess a genetic potential to harden that apparently evolved in cold climates (Sakai 1970). In contrast, taxa that evolved in maritime climates with mild and wet winters including subalpine and alpine shrubs of New Zealand (Sakai and Wardle 1978), Australia (Sakai *et al*. 1980), and the East Himalaya (Sakai and Malla 1981), do not possess a high level of hardiness.

Arctic and alpine populations of wide-ranging dwarf shrub taxa are typically hardy during the summer to <-5°C and during the winter to <-40°C (Tranquillini 1963, 1964; Bieble 1968; Sakai and Otsuka 1970; Somers 1981). Most alpine species are similarly hardy during the summer (Ulmer 1937, Pisek and Schiessl 1946), a requisite in cold, tundra environments. However, some differ in their potential to harden during the winter which may reflect floristic history. The cold hardiness of *C. mertensiana* and *C. tetragona* correlates with their habitat restrictions in the Canadian Rocky Mountains and their overall geographic distributions. *Cassiope mertensiana*, similar to many other taxa with maritime distributions, has a low level of cold hardiness and is restricted to areas with mild winters or where deep snow accumulations limit exposure to low temperatures. The evolution of a high level of cold hardiness in *C. tetragona* may have allowed its spread into cold arctic and continental alpine regions. Most other members of the genus and the growth form may be excluded from these areas of low and variable precipitation, low air temperatures, and generally severe winter conditions.

F. Integration

Differences in the physiological tolerances of these heath species are responsible for their niche separation in the Canadian Rocky Mountains. Winter microenvironments impose stringent constraints on plant survival while summer microenvironments influence plant growth and vigor (Table 21). *Cassiope mertensiana* is restricted to protected sites of early and deep snow accumulation where winter desiccation and cold temperature injury are avoided. Late snow release provides a more favorable summer soil moisture regime conducive to greater photosynthesis and growth. *Cassiope tetragona* occupies more exposed sites because of a greater

TABLE 21: Summary of factors influencing the success of Cassiope in various microenvironments in the Canadian Rocky Mountains. Microenvironments are as follows: 1. Fellfield--little or no snow; 2. Dryas-lichen, cushion plants--shallow and intermittant snow; 3. Cassiope tetragona-Dryas--moderate snow; 4. Cassiope mertensiana--deep snow; 5. Carex nigricans--deep and persistent snow.

C. MERTENSIANA		C. TETRAGONA	
WINTER	SUMMER	WINTER	SUMMER
1. NO SURVIVAL LOW TEMPERATURE AND DESICCATION INJURY WIND EROSION OF EXPOSED (ERECT) TISSUES	1. NO WINTER SURVIVAL	1. NO SURVIVAL DESICCATION INJURY WIND EROSION OF EXPOSED (ERECT) TISSUES	1. NO WINTER SURVIVAL
2. NO SURVIVAL LOW TEMPERATURE AND DESICCATION INJURY WIND EROSION OF EXPOSED (ERECT) TISSUES	2. NO WINTER SURVIVAL	2. NO LONG-TERM SURVIVAL YEARLY DESICCATION INJURY WIND EROSION OF EXPOSED (ERECT) TISSUES	2. NO LONG-TERM SURVIVAL DUE TO WINTER MORTALITY
			2-3. ENHANCED GROWTH BUT REDUCED SURVIVAL
3. NO LONG-TERM SURVIVAL LOW TEMPERATURE AND DESICCATION INJURY DUE TO UNRELIABLE SNOW COVER	3. NO LONG-TERM SURVIVAL DUE TO WINTER MORTALITY	3. NORMAL SURVIVAL APICES SURVIVE DESICCATION IN YEARS OF SHALLOW OR DELAYED SNOW COVER	3. OPTIMAL GROWTH AND FLOWERING NEW LEAVES TOLERANT OF SOIL AND ATMOSPHERIC MOISTURE STRESS NO SEEDLING ESTABLISHMENT
	3-4. SEASONAL CARBON GAINS REDUCED DUE TO WINTER MORTALITY, SOIL AND ATMOSPHERIC MOISTURE STRESS, REDUCED GROWTH AND LEAF LONGEVITY REDUCED FLOWERING NO SEEDLING ESTABLISHMENT		
4. NORMAL SURVIVAL NO WINTER MORTALITY	4. OPTIMAL GROWTH AND FLOWERING NO SEEDLING ESTABLISHMENT	4. ENHANCED SURVIVAL NO WINTER MORTALITY	4. EXTENDED LEAF LONGEVITY REDUCED GROWTH INTERSPECIFIC COMPETITION NO SEEDLING ESTABLISHMENT
4-5. REDUCED SURVIVAL DUE TO MICROTINE GRAZING	4-5. EXTENDED LEAF LONGEVITY REDUCED GROWTH AND INCREASED BRANCHING RESULTS IN STUNTED PLANTS REDUCED FLOWERING AND FRUIT MATURATION INCREASED POTENTIAL OF SEEDLING ESTABLISHMENT		4-5. REDUCED GROWTH RESULTS IN STUNTED PLANTS REDUCED FLOWERING AND FRUIT MATURATION INCREASED POTENTIAL OF SEEDLING ESTABLISHMENT
5. NO WINTER MORTALITY	5. NO LONG-TERM SURVIVAL DUE TO SHORT GROWING SEASON	5. NO WINTER MORTALITY	5. NO LONG-TERM SURVIVAL DUE TO SHORT GROWING SEASON

tolerance to summer atmospheric and soil moisture stress, winter desiccation, and low temperatures. It is not restricted from *C. mertensiana* habitats due to an intolerance of shortened growing periods *per se*, although "competitive ability" is probably reduced in such sites.

The tolerances of these species influence their overall geographic distribution. *Cassiope mertensiana* is restricted to maritime regions with mild winters and deep, dependable snow cover. In areas such as the Olympic Mountains, Sierra Nevada, and the Cascade Ranges where summers are warm and dry, it is highly restricted to microsites where delayed snow release and meltwaters help alleviate summer drought. Climatic variability increases in continental regions and it is restricted to more protected areas below treeline, i.e. habitats of greater environmental stability. *Cassiope tetragona* has evolved greater physiological tolerances and is thus more widespread in continental, alpine regions (Rocky Mountains) and the Arctic.

Dwarf shrub heath species are able to transgress treeline in the warmer, more protected microenvironments near the ground, but are limited at higher elevations and latitudes by many of the same factors that limit tree growth. In the low alpine and Low Arctic they are restricted to intermediate sites along mesotopographic gradients where extreme environmental conditions are avoided. The evergreen habit conveys certain advantages related to plant carbon and nutrient balance but a requisite to plant survival is a low mortality of evergreen tissues during winter. Habitats that are too exposed, i.e. accumulate less than a moderate snow cover in normal years, subject plants to lethal stresses during unusually dry winters. Evergreen dwarf shrubs have low growth rates, depend upon vegetative growth rather than sexual reproduction to maintain local populations, and have a low potential for recolonization, and thus can only persist where the winter survival of tissues is assured. Climatically severe tundra environments prohibit the maintenance of erect evergreen tissues that project above the snow or boundary layer near the surface. Evergreen species that survive in wind-exposed tundra habitats have evolved the cushion habit and greater tolerances to drought and low temperatures. Although they share with Cassiope many of the same physiological response patterns and conservative features, the prostrate form avoids some of the environmental adversity experienced by the erect shrubs. At the other end of the exposure gradient exists a tension zone where the length of the growing season determines summer carbon gains and long-term plant maintenance. In habitats of extremely late snow release the evergreen dwarf shrub habit is at a disadvantage and graminoids or forbs which posses high photosynthetic capacities and a different allocation strategy are favored.

This study contributes to a better understanding of an important taxon of treeline environments. Differences in species tolerances to water and low temperature stress are described which help explain vegetation patterns and geographic distributions, and suggest constraints to growth and survival of the growth form in severe tundra environments. Questions have been raised concerning the adaptive significance of leaf sclerophylly and the conservative growth habit that suggest future areas of research with these and other dwarf shrub heath species.

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APPENDIX A

Climatic data for Jasper townsite: "Normals", 1973, 1974, and 1975.

Table 22. Climatic "Normals" (1926-1975 unless indicated) for Jasper townsite, 52°53'N, 118°04'W, 1061m above mean sea level. Source: Atmospheric Environment Service Tables.

		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
Mean Daily Temperature	°C	-11.8	-7.0	-2.7	3.4	8.7	12.5	15.1	14.1	10.1	4.7	-3.6	-8.7	2.9
Mean Daily Maximum	°C	-6.7	-0.9	3.4	9.8	16.0	19.6	22.8	21.7	17.1	10.5	0.9	-4.1	9.2
Mean Daily Minimum	°C	-16.9	-13.0	-8.8	-3.1	1.4	5.4	7.4	6.6	3.1	-1.1	-8.2	-13.2	-3.4
Extreme Maximum	°C	13.3	15.0	20.0	25.6	29.4	32.8	36.7	35.0	31.1	27.2	16.7	15.0	36.7
Extreme Minimum	°C	-46.7	-43.3	-36.7	-28.9	-13.9	-6.7	-1.7	-2.8	-11.1	-21.7	-36.1	-42.2	-46.7
Mean Total Precipitation	mm	31.2	23.1	16.8	20.3	31.5	51.4	50.8	48.4	35.3	31.8	30.7	30.0	401.3
Mean Rainfall	mm	2.4	2.1	3.6	12.0	28.6	51.4	50.8	48.4	34.5	26.8	9.1	5.0	274.7
Mean Snowfall	cm	32.1	22.6	14.0	8.7	2.6	tr.	0	0	7.1	4.9	24.0	27.0	143.0
% Precipitation as Snow		92.3	90.9	78.6	40.9	9.2	0	0	0	2.3	15.7	70.4	83.3	31.5
Mean No. Days with Measurable ppt. (1926-70)		12	9	7	8	9	13	13	13	10	10	10	12	126
Mean No. Days with Measurable Rain (1926-70)		1	1	1	5	9	13	13	13	10	9	3	2	80
Mean No. Days with Measurable Snow (1926-70)		11	8	7	4	1	0	0	0	tr.	2	8	11	52

Table 23. Climatic data for Jasper townsite: 1973. Source: Atmospheric Environment Service Tables.

		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
Mean Daily Temperature	°C	-9.6	-6.4	0.3	3.2	9.0	11.7	14.8	14.2	10.7	3.6	-11.3	-7.4	2.7
Mean Dialy Maximum	°C	-4.4	-1.0	5.0	9.4	16.5	18.2	22.9	22.1	17.4	7.7	-7.3	-3.2	8.6
Mean Daily Minimum	°C	-14.7	-11.9	-4.5	-3.1	1.5	5.2	6.8	6.3	3.9	-0.5	-15.3	-11.8	-3.2
Extreme Maximum	°C	7.8	12.2	11.1	18.3	28.9	30.0	31.1	31.7	28.3	14.4	3.3	3.9	31.7
Extreme minimum	°C	-33.9	-27.2	-11.1	-13.3	-4.4	-1.7	2.8	-1.1	-4.4	-8.9	-24.4	-26.1	-33.9
Total Precipitation	mm	23.4	9.7	18.0	22.9	24.9	31.5	15.2	38.4	22.4	39.9	50.3	10.9	307.3
Rainfall	mm	2.8	tr.	1.8	14.0	24.9	31.5	15.2	38.4	22.4	28.2	tr.	tr.	179.1
Snowfall	cm	30.5	12.7	22.6	12.5	tr.	0	0	tr.	tr.	13.5	70.9	14.7	177.3
% Precipitation as Snow		88.0	100	90.0	38.9	0	0	0	0	0	29.3	100	100	41.7
No. Days with Measurable ppt.		11	9	11	8	8	11	11	10	13	17	17	10	136
No. Days with Measurable Rain		4	0	2	6	8	11	11	10	13	14	0	0	79
No. Days with Measurable Snow		10	10	11	7	0	0	0	0	0	8	19	12	77

Table 24. Climatic data for Jasper townsite: 1974. Source: Atmospheric Environment Service Tables.

		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
Mean Daily Temperature	°C	-15.1	-3.7	-4.6	5.1	7.0	13.2	13.8	14.3	9.8	6.3	-3.4	-3.9	3.2
Mean Dialy Maximum	°C	-10.2	1.7	1.5	11.4	12.6	20.6	21.2	21.4	17.4	12.2	1.1	0.5	9.3
Mean Daily Minimum	°C	-19.9	-9.2	-10.6	-1.2	1.3	5.7	6.4	7.3	2.1	0.4	-7.9	-8.4	-2.8
Extreme Maximum	°C	6.1	7.2	11.7	22.2	19.4	30.0	30.6	32.8	26.7	21.1	11.7	6.7	32.8
Extreme Minimum	°C	-35.6	-24.4	-23.3	-5.6	2.2	-1.7	2.2	-2.2	-4.4	-5.6	-22.2	-21.1	-35.6
Total Precipitation	mm	87.9	9.7	22.1	16.0	25.1	32.5	54.4	25.1	28.7	24.9	34.5	15.5	376.4
Rainfall	mm	0	0	tr.	11.4	17.0	32.5	54.4	25.1	28.7	21.6	1.3	tr.	192.0
Snowfall	cm	117.4	11.9	27.4	4.3	8.6	0	0	0	tr.	3.3	45.2	19.3	237.5
% Precipitation as Snow		100	100	100	28.8	32.3	0	0	0	0	13.3	96.2	100	49.0
No. Days with Measurable ppt.		21	10	15	10	15	12	15	11	9	9	11	9	147
No. Days with Measurable Rain		0	0	0	8	14	12	15	11	9	7	2	0	78
No. Days with Measurable Snow		22	12	15	2	5	0	0	0	0	2	10	10	78

Table 25. Climatic data for Jasper townsite: 1975. Source: Atmospheric Environment Service Tables.

		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
Mean Daily Temperature	°C	-10.6	-13.3	-4.7	1.9	8.2	11.3	17.3	12.2	11.5	3.6	-4.0	-8.2	2.1
Mean Dialy Maximum	°C	-5.6	-7.4	1.1	9.0	15.1	17.3	24.8	17.7	19.8	8.4	0.3	-3.8	8.1
Mean Daily Minimum	°C	-15.5	-19.2	-10.5	-5.2	1.3	5.3	9.7	6.7	3.2	-1.2	-8.3	-12.7	-3.9
Extreme Maximum	°C	3.3	7.2	8.3	18.3	22.2	24.4	33.9	25.0	27.2	23.9	16.1	6.1	33.9
Extreme minimum	°C	-37.2	-33.3	-21.7	-16.7	-3.3	-1.7	2.8	1.7	-2.2	-8.3	-27.8	-27.2	-37.2
Total Precipitation	mm	11.7	18.0	8.9	4.1	31.0	72.4	21.8	76.7	18.0	36.8	47.0	42.2	388.6
Rainfall	mm	tr.	0.3	tr.	4.1	28.4	72.4	21.8	76.7	18.0	25.7	33.5	3.6	284.5
Snowfall	cm	16.3	21.1	14.0	tr.	2.3	0	0	0	0	11.7	14.0	62.0	141.2
% Precipitation as Snow		100	98.3	100	0	8.4	0	0	0	0	30.2	28.7	91.5	26.8
No. Days with Measurable ppt.		9	8	8	2	13	19	9	21	5	15	13	12	134
No. Days with Measurable Rain		0	1	0	2	13	19	9	21	5	12	6	4	92
No. Days with Measurable Snow		12	8	10	0	2	0	0	0	0	4	9	13	58

APPENDIX B

Soil profile descriptions for Sites 3, 4, and 5.

Table 26. Soil profile description at Site 3.

Site 3 is located at 2010 m on a 25% N slope. The well to moderately well drained pedon supports a *Picea-Abies* closed forest with a dense shrub understory of *C. mertensiana* and *Vaccinium scoparium* in small openings. Glacial till has been mixed by colluvial action. Frost hummocks are common.

Horizon	Depth (cm)	Description
Site 3. (*C. mertensiana-Vaccinium*): Orthic Dystric Brunisol		
L	6-0	Fibrous turf; abundant, very fine to coarse random roots; abrupt, smooth boundary; 4-8 cm thick.
Bmy	0-22	Very dark grayish brown (10 YR 3/2 m, 5/2 d) sandy loam; very weak, fine subangular blocky; loose, very friable; very few, very fine random roots and few, fine to coarse horizontal roots; abundant, gravel and cobbles at lower boundary; clear, irregular boundary; 10-22 cm thick; strongly acid. Discontinuous organic layer (8 cm thick) at 14 cm depth.
C	22 +	Dark grayish brown (2.5 Y 4/2 m, 6/4 d) sandy loam; amorphous; very friable; some, gravel and cobbles; strongly acid. Frozen soil at 53 cm depth on July 26, 1973.

Table 27. Soil profile descriptions at Site 4.

Site 4 is located at 2135 m on a 24% N slope. The rapidly to well drained (*C. tetragona*-*Dryas*) and moderately well drained (*C. mertensiana*) pedons support communities of *Cassiope* spp. in different microsites (See Figure 7). Glacial till has been deposited on Precambrian sandstones, conglomerates, siltstones, and slates, and mixed by colluvial action. Some aeolian deposits may be present in depressional areas. Frost hummocks (to 50 cm height) abundant in *C. mertensiana* microsite, with frequent mixing of Ah and Bm horizons.

Horizon	Depth (cm)	Description
Site 4. (*C. tetragona*-*Dryas*): Orthic Dystric Brunisol		
L	2-0	Fibrous turf; abundant, very fine to medium roots and few, coarse roots; abrupt, wavy boundary; 0-3 cm thick.
Ah	0-3	Black (10 YR 2/1 m, 3/2 d) sandy loam; very weak, fine subangular blocky; loose, very friable; plentiful, very fine to medium random roots and few, coarse roots; clear, irregular boundary; 2-10 cm thick; strongly acid.
Bmy	3-12	Very dark grayish brown (10 YR 3/2 m, 4/3 d) sandy clay loam; very weak, fine subangular blocky; loose, very friable; few, very fine to medium horizontal roots; few, angular gravel at lower boundary; clear, irregular boundary; 6-12 cm thick; strongly acid.
C	12 +	Olive brown (2.5 Y 4/3 m, 6/3 d) sandy loam; amorphous; very friable; abundant, angular gravel; strongly acid.
Site 4. (*C. mertensiana*): Orthic Dystric Brunisol		
L	3-0	Fibrous turf; abundant, very fine to medium roots; abrupt, smooth boundary; 3-4 cm thick.

Table 27. (continued)

Horizon	Depth (cm)	Description
Ah	0-7	Very dark gray (10 YR 3/1 m, 4/2 d) loamy sand; very weak, fine subangular blocky; loose, very friable; plentiful, very fine to medium random roots; clear, irregular boundary; 7-10 cm thick; extremely acid.
Bmy1	7-13	Brown (10 YR 4/3 m, 5/3 d) sandy clay loam; very weak, fine subangular blocky; loose, very firable; few, fine horizontal and oblique roots; clear, wavy boundary; 4-7 cm thick; very strongly acid.
Bmy2	13-17	Very dark grayish brown (10 YR 3/2 m, 5/2 d) sandy clay loam; very weak, fine subangular blocky; loose, very friable; few, fine horizontal and oblique roots; abrupt, wavy boundary; 3-7 cm thick; very strongly acid.
Cgj	17 +	Olive brown (2.5 Y 4/3 m, 6/3 d) sandy clay loam; common, fine, distinct reddish mottles above cobbles; amorphous; very friable; few, fine roots; some, gravel and cobbles; very strongly acid. Frozen soil at 50 cm depth on July 27, 1973.

Table 28. Soil profile descriptions at Site 5.

Site 5 is located at 2225 m along the summit ridge on a 5% N slope. These rapidly drained pedons support *C. tetragona*-*Dryas* in slightly depressional microsites and grade rapidly into stony pavement, scree, or surficial bedrock with very scattered plants of *Dryas*, *Oxytropis*, and *C. tetragona*. Precambrian sandstones and conglomerates are covered by varying thicknesses of colluvium in depressional microsites. Some aeolian deposits may be present.

Horizon	Depth (cm)	Description
Site 5. (*C. tetragona*-*Dryas*): Orthic Dystric Brunisol		
LFH	6-0	Fibrous turf; abundant, fine to medium random roots; abrupt, smooth boundary; 4-7 cm thick.
Ah	0-6	Very dark gray (10 YR 3/1 m, 4/2 d) loamy sand; very weak, fine subangular blocky; loose, very friable; few, fine roots; clear, broken boundary; 6-10 cm thick; very strongly acid.
Bm1	6-12	Very dark grayish brown (10 YR 3/2 m, 4/3 d) sandy clay loam; very weak, fine subangular blocky; loose, very friable; very few, fine roots; clear, smooth boundary; 3-12 cm thick; very strongly acid.
Bm2	12-13	Brown (10 YR 4/3 m, 5/4 d) sandy clay loam; very weak, fine subangular blocky; loose, very friable; clear, smooth boundary; 1-2 cm thick; strongly acid.
C	13 +	Olive brown (2.5 Y 4/3 m, 6/3 d) sandy loam; amorphous; very friable; some, gravel and cobbles; strongly acid.

Table 28. (continued)

Horizon	Depth (cm)	Description
Site 5. (Stony pavement-widely spaced plants): Orthic Regosol		
Ah	0-3	Very dark gray (10 YR 3/1 m, 5/2 d) sand; very weak, fine subangular blocky; loose, very friable; abundant, very fine to fine random roots; abundant, gravel and cobbles; clear, wavy boundary; 2-4 cm thick; medium acid.
C	3-20	Olive brown (2.5 Y 4/3 m, 6/3 d) loamy sand; amorphous; very friable; abundant, gravel and cobbles; strongly acid.
R	20 +	Bedrock